TRANSACTIONS

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SAN DIEGO SOCIETY OF NATURAL HISTORY

EVOLUTION OF THE PIT VIPERS

BY

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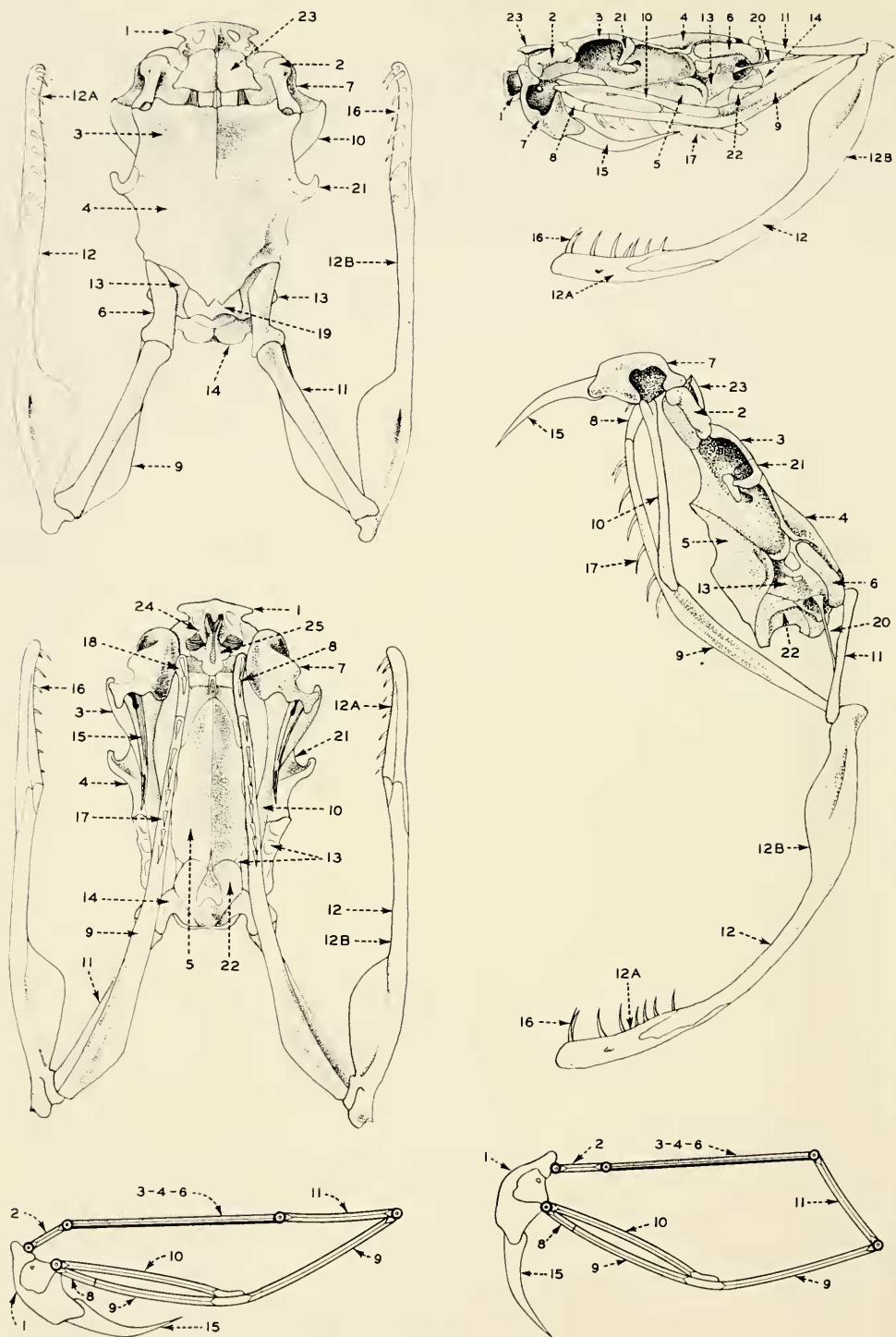Fullerton, California*

Fig. 1. Skull of *Crotalus ruber ruber*. From Klauber, 1956.

Key to bones: 1, Premaxilla; 2, Prefrontal; 3, Frontal; 4, Parietal; 5, Basisphenoid; 6, Squamosal; 7, Maxilla; 8, Palatine; 9, Pterygoid; 10, Ectopterygoid; 11, Quadrate; 12, Mandible (or lower jaw); 12A, Dentary; 12B, Articular; 13, Pro-otic; 14, Exoccipital; 15, Poison fang; 16, Mandibular teeth; 17, Pterygoid teeth; 18, Palatine teeth; 19, Supraoccipital; 20, Stapes; 21, Postfrontal; 22, Basioccipital; 23, Nasal; 24, Turbinal; 25, Vomer.

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CONTENTS

INTRODUCTION

The skeleton is one of the most important structures available for the analysis of relationships of vertebrates. This paper assesses relationships within one group of vertebrates, the Crotalidae, by a study of their comparative osteology.

The Crotalidae, or pit vipers, of America and Eurasia, is a family of poisonous snakes with movable fangs. The Crotalidae shows remarkable parallel evolution with the Old World family of true vipers, the Viperidae. The Crotalidae differs from the Viperidae in many characters, the most conspicuous of which is the presence of heat-sensitive facial pits.

The Crotalidae, as currently defined, includes six genera: *Crotalus* (rattlesnakes; North, Central, and South America), *Sistrurus* (pigmy rattlesnakes; North America), *Lachesis* (bushmaster; Central and northern South America, Trinidad), *Bothrops* (fer-de-lance, hog-nosed pit vipers, palm pit vipers; Mexico, Central and South America), *Trimeresurus* (Asiatic pit vipers; southeast Asia), and *Agkistrodon* (copperheads, moccasins; North America, Asia, and extreme southeastern Europe).

TABLE 1

Summary of material examined.

Genus	Species in genus	Species examined	Skeletons Examined
Agkistrodon	14	9[1]	50
Bothrops	30?	13	40
Crotalus	24	23[2]	281
Lachesis	1	1	7
Sistrurus	3	3	21
Trimeresurus	33	8	15
Totals	105	57	414

[1]Not examined: *A. annamensis, himalayanus, millardi, monticola, nepa.*
[2]Not examined: *C. transversus.*

MATERIALS AND METHODS

In the course of this study, skeletons of crotalids were borrowed from most of the major museums in the United States. A report on the fossil material has been given elsewhere (Brattstrom, 1954). The recent material examined is listed in tables 1 to 3. Skeletons of several species of the Viperidae were also examined. Through the courtesy of curators at several museums, I was allowed to remove the skulls of rare crotalids from preserved specimens. This can be done without damage to any of the scales, and the skull can be replaced with cotton. References to individual specimens use standard abbreviations for names of institutions.

Measurements were made to the nearest tenth of a millimeter with a vernier caliper. Paired bones were measured consistently on the more convenient side (*e.g.*, the frontal and ectopterygoid on the right side, the pterygoid on the left) except when one member of a pair was absent. No significant difference was noted in measurements of paired bones. Klauber (1939) found the same with regard to fangs.

The skeletons examined had been prepared in many ways. Bones that had remained too long in bleach had rough edges; these bones were not measured. Specimens that had been in formaldehyde for many years often had soft bones, and these also were not measured. Except for these two easily detected conditions, the skeletons examined showed no differences resulting from method of preparation.

Drawings were made of most bones of each skeleton examined. The mode or the most typical example of each skull bone of each species is illustrated herein. Measurements of length and width were graphed as were ratios of measurements of one bone to measurements of another (*e.g.*, quadrate length to pterygoid length). Graphs were made for all bones measured and for almost all possible combinations of them. Only a few of these graphs are reproduced here, though most of them are discussed.

The terms and names used are those of recent authors on each group or geographic area: Cochran, 1943; Gloyd, 1940; Gloyd and Conant, 1943; Klauber, 1936a, 1949, 1952, 1956; Maslin, 1942; Pope, 1935; Pope and Pope, 1933; Rooij, 1917; Schmidt, 1953; M. A. Smith, 1931.

ACKNOWLEDGMENTS

TABLE 2

Specimens examined: *Agkistrodon, Bothrops, Lachesis, Sistrurus,* and *Trimeresurus.*

Animal	Number	Animal	Number	Animal	Number
Agkistrodon	50	*Bothrops*	40	*Sistrurus*	21
acutus	1	alternata	2	catenatus ssp.	6
bilineatus	5	atrox	18	catenatus	4
blomhoffi	2	bilineatus	1	tergeminus	1
contortrix ssp.	8	cotiara	1	miliarius ssp.	4
laticinctis	1	dunni	1	streckeri	1
contortrix	1	godmani	2	ravus	5
mokeson	3	jararaca	4	*Trimeresurus*	15
halys	2	jararacussu	4	albolabris	1
hypnale	1	lanceolatus	1	flaviviridis	2
piscivorus ssp.	8	nasuta	1	gramineus	1
leucostoma	9	neuwiedi	2	mucrosquamatus	1
piscivorus	7	nummifer	1	puniceus	1
strauchi	1	schlegeli	1	purpureomaculatus	2
rhodostoma	1	*Lachesis muta*	7	stejnegeri	1
				wagleri	6

COMPARATIVE OSTEOLOGY OF THE CROTALIDAE

GENERAL OSTEOLOGICAL OBSERVATIONS

The osteology of various crotalids has been described by Tyson (1683), Owen (1853), Giebel (1866), Hoffman (1890), W. E. Taylor (1895), Boulenger (1896), Gadow (1920), Phisalix (1922), Klauber (1936a, 1939, 1956), Radovanovic (1937), M. A. Smith (1943), and Ruiz (1951). Most of these descriptions are concerned primarily with the fang mechanism, poison apparatus, or family characterization. Skulls of crotalids were figured by Ditmars, 1931

TABLE 3
Specimens of *Crotalus* examined.

Animal	Number	Animal	Number	Animal	Number
adamanteus	22	*atricaudatus*	5	*pusillus*	5
atrox	38	*intermedius*	1	*ruber*	20
basiliscus	5	*lepidus* ssp.	2	*scutulatus*	8
cerastes ssp.	6	*lepidus*	2	*stejnegeri*	2
cerastes	6	*klauberi*	3	*tigris*	2
laterorepens	17	*mitchelli*		*tortugensis*	1
durissus		*mitchelli*	2	*triseriatus*	3
durissus	4	*pyrrhus*	13	*viridis* ssp.	1
terrificus	5	*stephensi*	1	*decolor* (= concolor)	1
tzabcan	5	*molossus*		*helleri*	31
unicolor	2	*molossus*	7	*oreganus*	12
enyo	5	*nigrescens*	1	*lutosus*	4
horridus ssp.	3	*polystictus*	1	*viridis*	17
horridus	11	*pricei*	4	*willardi*	3

(*Lachesis*) and 1933 (*Lachesis, B. atrox, C. adamanteus*); Gadow, 1920 (*C. "durissus"*[1]); Phisalix, 1912, 1914, 1922 (*Lachesis*); Radovanovic, 1937 (*C. horridus, A. contortrix, A. blomhoffi, T. wagleri, B. atrox*); H. M. Smith, 1946 (*C. intermedius, C. gloydi, C. triseriatus*); M. A. Smith, 1943 (*A. rhodostoma*); and Steindachner, 1913 (*T. mucrosquamatus*). The vertebrae have been discussed from the viewpoints of myology (Mosauer, 1935), evolution (Johnson, 1955a, 1955b, 1956), osteology (de Rochebrune, 1881; Goette, 1897), and paleontology (Simpson, 1933; Gilmore, 1938; Brattstrom, 1953, 1954, 1955, 1958). The shaker (or style) of rattlesnakes has been described in some detail by Zimmermann and Pope (1948). The general anatomy of the skull and vertebrae of a rattlesnake were fully described and illustrated by Klauber (1956). Some of Klauber's illustrations are reproduced here (figs. 1, 2).

Anomalies, Diseases, and Injuries

Injured bones were relatively rare among the skeletons examined in this study. The most common abnormality seen was the fusion of several vertebrae. Another abnormality or injury found was the enlargement of the bone at the junction of the dentary with the angular and splenial. The lower jaw is probably the weakest group of bones in the snake's body, and the dentary junction seems to be especially fragile. It is possible that fracture of the bones of the lower jaw occurs during striking or during the eating of oversized prey. A double squamosal bone was found on each side of the head of one specimen of *Crotalus horridus*.

Ontogenetic Variation

Small variations were noted in the shapes of certain bones and processes. Some of these variations appeared to be ontogenetic, but most appeared to be individual or geographic variations. Study of variation in species represented by large samples (such as *A. contortrix, A. piscivorus, B. atrox, C. atrox, C. cerastes, C. ruber, C. viridis, T. wagleri*) helped evaluate differences found in species of which few specimens were available.

There is no major change in the shape of the various bones of the skull of crotalids after birth. Cranial bones become strongly ossified during the first or second year. After ossification, the bones increase in size with the general growth of the snake. In a series of 11 new-born *Bothrops atrox* from a single brood from Panama, there was very little variation in the skulls. These individuals did not differ greatly from the adults except in three characters: the dorsal surface of the parietal had not yet become completely ossified and was triangular and arched; the ectopterygoid was not greatly forked; and the ventral process of the basisphenoid had not yet developed.

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[1]The figure looks like *C. horridus,* however. In one of the drawings there are four teeth in the left pterygoid, in two other drawings, supposedly of the same individual, there are five.
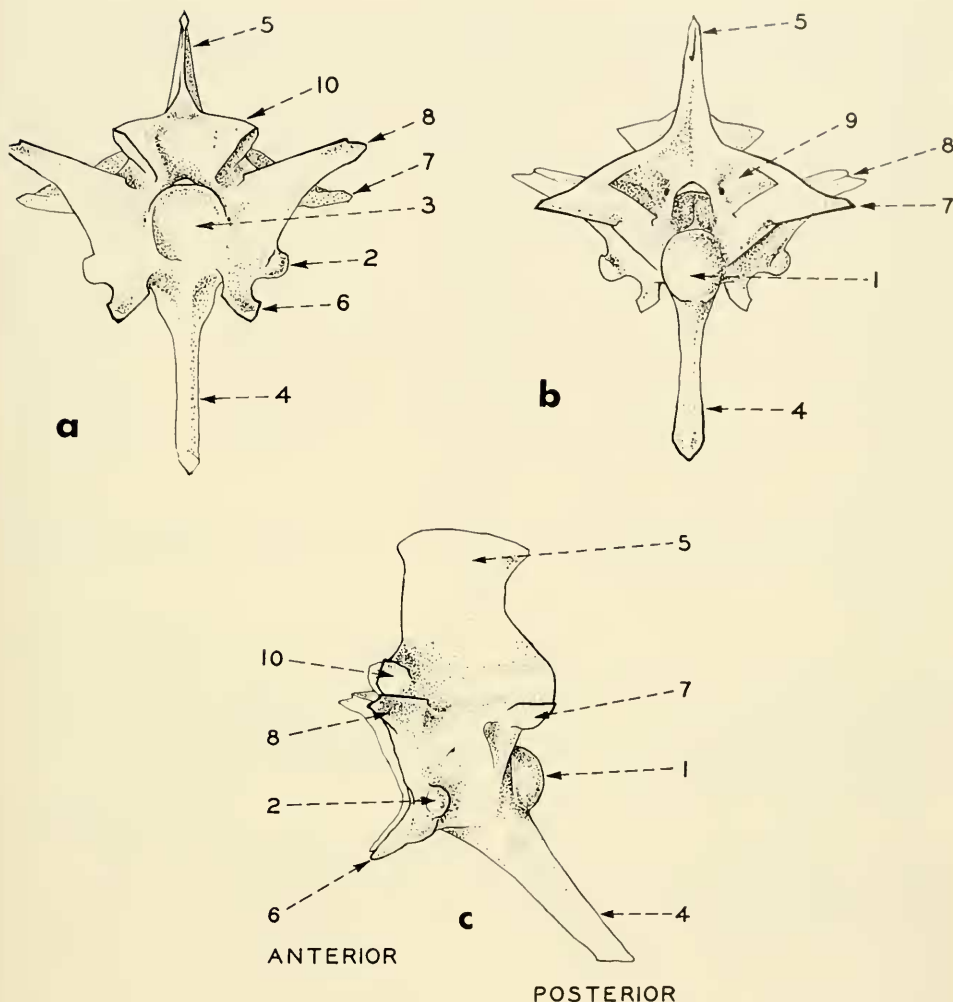
Fig. 2. Mid-thoracic vertebra of *Crotalus ruber ruber*. From Klauber, 1956. a, front view; b, rear view; c, side view.

Key to parts: 1, Condyle or ball of centrum; 2, Diapophysis; 3, Cup of centrum; 4, Hypapophysis; 5, Neural spine; 6, Parapophysis; 7, Postzygapophysis; 8, Prezygapophysis; 9, Zygantrum; 10, Zygosphene.

Most crotalids show little ontogenetic change; however, *Lachesis muta* apparently is an exception. If the lines of *Lachesis* measurements are extrapolated backward on the various graphs, they do not conform with the size changes shown in the other genera of the family. It is therefore apparent that either there is ontogenetic change in relative lengths of bones in this species, or the young hatch extremely large.

Because bone dimensions increase with age, it is useful to have some standard reference with which to compare measurements. Since fang length and head length were measurable on most skulls examined, these were used as a basic index of age. The "head length" measured on preserved specimens by Klauber (1937, 1938, 1939) differs by only a few millimeters (the thickness of the skin) from the "lower jaw length" used here.

TABLE 4

Counts of tooth sockets in *Agkistrodon*, showing number of specimens[1], (range), and mean.

Species	Palatine	Pterygoid	Dentary
acutus	2(4)4	2(13)13	2(17-18)17.5
bilineatus	10(3-5)3.8	10(14-17)15.1	9(16-18)16.2
blomhoffi	2(4)4	2(12)12	2(11-12)11.5
contortrix	22(4-5)4.4	24(12-21)16.1	19(12-17)15.1
halys	2(3-5)3.5	3(9-13)11.3	4(12-13)12.3
hypnale	2(4)4	2(15-16)15.5	2(17)17
piscivorus ssp.	10(5)5	15(13-16)14.9	15(16-20)18.3
piscivorus	14(4-5)4.9	14(13-17)15.1	14(18-21)18.6
leucostoma	17(4-5)4.9	16(14-18)15.4	12(16-18)17.8
total	41(4-5)4.9	45(13-18)15.1	41(16-21)18.2
strauchi	1(3?)3?	2(7-8)7.5	2(10-11)10.5
Total	82(3-5)4.3	90(7-21)13.6	81(10-21)15.5

[1] In tables 4-7, the number of specimens is the number of bones with countable sockets, not the number of skulls. Occasionally the paired bones differed by one or two sockets, and occasionally a tooth-bearing bone was lost or broken on one side of the skull.

At the suggestion of L. M. Klauber, I tested the methods used by Bryuzgin (1939), Petter-Rousseaux (1953) and Senning (1940) for determining the age of reptiles and amphibians by counting growth rings in bones. Most of the bones of crotalids show a series of light and dark rings. These are most evident and most easily counted on the neural spines and the ectopterygoid and articular bones and particularly on the frontal bone. Counts of the number of rings on each of these bones from one individual were the same.

The southern California population of *Crotalus viridis helleri* is relatively homogeneous (Klauber, 1936b, 1937, 1945, 1949). When ring counts on skulls from this population were plotted on a log-log scale against head length and against fang length, S-shaped growth curves resulted. Similar data from another relatively homogeneous series (*C. viridis oreganus* from Washington and Idaho; Klauber, *supra cit.*) resulted in very similar curves. Similar data for other species of *Crotalus* show the same type of growth curves as for *C. viridis,* though the slopes of the curves, and hence probably the rates of growth, are different for the different species examined.

The greatest number of rings counted in a rattlesnake born in captivity with the skull available was 16, though *C. viridis* has been kept in captivity for 19 years (Shaw, 1957).

These data plus the conclusions reached by Peabody (1958, 1961) and by Senning, Bryuzgin, and Petter-Rousseaux (*supra cit.*) suggest that these rings are useful for the determination of age and may, in fact, be growth rings, one added per year.

Geographic Variation

Small geographic variations were noted in size and shape of certain bones and processes. In general, the variation noted was minor; the skulls of any one species were usually very similar. The osteological similarities within species and differences between species were sufficiently constant, not only for characterization of species and determination of relationships, but also for construction of artificial keys to skulls (see Klauber, 1956). Although the variation found among individuals of local populations was small, a greater amount of variation was evident between widely separated populations of the same species. Some examples of geographic variation follow.

TABLE 5

Counts of tooth sockets in *Bothrops*, showing number of specimens, (range), and mean.
See footnote in table 4.

Species	Palatine	Pterygoid	Dentary
alternata	——	2 (10-11) 10.5	3 (10-12) 11
atrox: total	17 (3-5) 4.1	13 (13-18) 15.5	18 (14-19) 16.7
adults	10 (3-5) 4.2	7 (13-17) 15.7	11 (16-19) 16.8
young[1]	7 (4) 4	6 (14-18) 15.2	7 (14-18) 16.6
bilineatus	2 (5) 5	2 (17-18) 17.5	2 (17) 17
cotiara	1 (3?) 3?	2 (11-12) 11.5	2 (12-13) 12.5
godmani	2 (4) 4	4 (12) 12	4 (14-17) 15.3
jararaca	2 (4-5) 4.5	4 (15-17) 16.3	4 (6-17) 10.8
jararacussu	8 (3-5) 3.8	8 (14-17) 16.0	8 (13-18) 15.4
lanceolatus	2 (2) 2	2 (10-11) 10.5	2 (12-13) 12.5
nasuta	——	2 (10-11) 10.5	2 (12) 12
neuwiedi	4 (3-4) 3.5	4 (10-12) 11.5	4 (10-13) 11.5
nummifer	2 (4) 4	2 (13-14) 13.5	2 (14-15) 14.5
schlegeli	2 (5) 5	2 (16) 16	2 (15-16) 15.5
Total	44 (2-5) 3.8	49 (10-18) 13.5	55 (6-19) 14

[1]New-born brood.

The nasal bone is variable in many crotalids, but some constancy apparently has developed in *Crotalus cerastes*. About 90 per cent of the skeletons of two subspecies can be distinguished. In *C. c. cerastes*, from the Mohave Desert, the nasal is square, whereas in *C. c. laterorepens*, from the Colorado Desert, it is elongate. No specimens were available of the Arizona form, *C. c. cercobombus*.

In *C. durissus terrificus* and *C. d. unicolor* the nasal bones are squarish, with anterolateral processes; in *C. d. tzabcan* they are squarish or rectangular, usually with posterolateral processes. The medial edge of the squamosal is usually straight in the former two and curved in the latter. The anterior hump of the process of the basisphenoid is usually low and rounded in *C. d. tzabcan* and well developed and pointed in *C. d. terrificus*.

To judge from the few skulls with subspecific or locality data, in *C. h. horridus* the basisphenoid process has a pointed anterior hump, while in *C. h. atricaudatus* the hump is absent or low.

Crotalus viridis varies in the width of the parietal, the curvature of the squamosal, and the shape of the dorsal process of the premaxilla. In *C. v. decolor* (= *concolor*), the parietal is a relatively elongate triangle, and the squamosal has straight sides except anteriorly, where it is curved. In *C. v. lutosus*, the parietal is almost an equilateral triangle, the squamosal has straight sides which taper anteriorly, and the dorsal process of the premaxilla is an elongate triangle. In *C. v. helleri* the parietal is an elongate triangle, the squamosal has curved sides, and the dorsal process of the premaxilla is thin and expands into a small triangle at its base. In *C. v. oreganus* from Washington and Idaho, the parietal is a broad triangle, the squamosal has straight sides, though somewhat curved and blunt anteriorly, and the dorsal process of the premaxilla is thin, with a broad triangle at its base. In one specimen of *C. v. oreganus* from the Sierra Nevada of California, the parietal is broader than usual, and the dorsal process of the premaxilla is a broad triangle. In *C. v. viridis* the parietal is a broad triangle, the squamosal has straight sides and is blunt anteriorly, and the dorsal process of the premaxilla is thin.

TABLE 6

Counts of tooth sockets in *Crotalus*, showing number of specimens, (range), and mean.
See footnote in table 4.

Species	Palatine	Pterygoid	Dentary
adamanteus	39 (1-3) 2.7	40 (7-11) 8.1	39 (9-10) 9.5
atrox	67 (3) 3	70 (7-9) 8	70 (7-11) 9.9
basiliscus	4 (0-2) 1	4 (7-8) 7.5	4 (9-11) 9.8
cerastes	44 (2-4) 3	46 (7-9) 8.4	45 (8-11) 9.8
durissus	18 (0-2) 1.1	12 (7-9) 7.8	14 (8-11) 9.8
enyo	6 (1-3) 2.7	2 (8) 8	4 (9-11) 10
horridus	28 (2-3) 2.9	34 (8-11) 8.7	34 (10-13) 10.9
intermedius	1 (3) 3	1 (5) 5	1 (8) 8
lepidus	7 (2-3) 2.7	8 (6-8) 6.9	10 (8-9) 8.1
mitchelli	15 (2-3) 2.9	24 (7-10) 8.2	23 (7-10) 8.9
molossus	12 (1-3) 2.1	12 (6-10) 8.8	9 (9-11) 10
polystictus	2 (0) 0	2 (7) 7	2 (8) 8
pusillus	9 (3) 3	9 (7-9) 7.7	10 (9-11) 10.1
pricei	3 (3) 3	5 (6-7) 6.6	3 (9-10) 9.3
ruber	27 (3) 3	26 (6-9) 8	31 (8-11) 9.5
scutulatus	16 (3) 3	16 (6-8) 7.3	14 (9-10) 9.6
stejnegeri	4 (0) 0	3 (4-5) 4.7	4 (6-7) 6.5
tigris	4 (3) 3	4 (7-9) 8	3 (9-10) 9.3
tortugensis	2 (3) 3	2 (9) 9	2 (10) 10
triseriatus	4 (3) 3	5 (6-7) 6.2	3 (7-8) 7.3
viridis: total	103 (2-4) 2.9	108 (6-10) 7.4	107 (6-11) 9.3
decolor	1 (3) 3	2 (6-7) 6.5	2 (9) 9
lutosus	8 (2-3) 2.5	6 (7-8) 7.2	6 (9-10) 9.3
helleri	47 (3) 3	52 (7-10) 7.8	50 (8-11) 9.4
oreganus	17 (2-4) 3.1	16 (6-9) 7.8	18 (9-10) 9.6
viridis	30 (2-3) 3	32 (7-9) 7.7	31 (6-11) 9.1
willardi	4 (1-2) 1.8	6 (5-7) 6.2	5 (8) 8
Totals	417 (0-4) 2.4	440 (4-11) 7.4	437 (6-13) 8.7

In one specimen of *Lachesis muta* from Colombia (AMNH 63419), the basisphenoid process is triangular, whereas in three specimens from Panama it is rectangular. In the Colombian specimen, the lower two processes of the prefrontal are not strongly fused, and the dorsal process is about equal to the middle process in length; the lower process is the shortest. In the Panamanian specimens, the lower two processes of the prefrontal are fused and are longer than the upper.

DESCRIPTIVE OSTEOLOGY

The osteology of each species is not described in detail, but rather is illustrated (figs. 15 to 32) and summarized (tables 10 to 12). In the tables, the various characters are listed for each species. The detailed descriptions of the bones, the variations noted, and the specific characters used, are given below. A summary of the tables, in terms of relationships, will be given beyond.

Teeth

In the Crotalidae, teeth are found on the maxilla, pterygoid, palatine, and dentary bones, with the fang in the maxilla. The fang has been fully discussed by Klauber (1939, 1956) and by H. M. Smith (1952). The fangs of the various crotalids are similar but differ slightly in length and curvature, and in the size and shape of the lumen (Klauber, 1939). *Trimeresurus wagleri* has the most atypical fang of any crotalid, for the lower lumen usually is on the inner or medial side, not on the anterior surface as in the rest of the crotalids. In one specimen of *T. wagleri*, however, the lower lumen is anteromedial.

In one specimen of *Lachesis muta* (BHB 1635) from Panama, one of the functional fangs has two lower lumen openings, one above the other, with a groove between them and another groove above the upper of the two. There are two functional fangs in each maxilla of one specimen of *Bothrops atrox* examined (USNM-NZP 4072).

The number of teeth was determined for each crotalid skull examined. As shown by Bogert (1943), accurate tooth counts can be obtained only by counting the sockets and not by just counting the teeth present. Counts of tooth sockets can be made on preserved specimens as well as on skeletons. Tooth socket counts for the crotalids examined are given in tables 4 to 7. The number of tooth sockets plotted against size of snake indicate that in crotalids there is no change in the number of teeth with age.

It is a general rule that more primitive vertebrates have a greater number of teeth. However, a large number of teeth can sometimes be a specialization, as in mosasaurs and porpoises. Since it is difficult to determine whether a large number of teeth is specialized or primitive among crotalids, little value was given to this character in determining relationships. It is interesting, however, that several crotalids have a small number of palatine teeth: *C. durissus*, *C. polystictus*, *C. stejnegeri*, *C. willardi*, *T. jerdoni*, and *T. flaviviridis* (tables 4-7).

Among species of crotalids that are relatively homogeneous in external characters, there is little variation in tooth counts, but in heterogeneous species, such as *C. viridis*, there is wide variation. Some species have extremely elongate, straight teeth, and others have short, stubby teeth. *Crotalus polystictus* is unusual in having extremely elongate, narrow dentary and pterygoid teeth, with the basal one-fourth of each tooth enlarged.

Bones

Premaxilla (Premaxillary). — The premaxilla (figs. 15, 16) of crotalids is T-shaped, with the cross-bar of the T forming the anterior ventral edge of the bone. The vertical part of the T forms a dorsal projection. This projection has a thin posterior process that acts as a septum between the nares. The anterior edge of the basal portion of the bone may be pointed, curved, or flat. The dorsal process may be thin, thick, or thick at the base and thin dorsally (see *C. atrox*, fig. 15). The premaxilla supports the rostral scale, and there appears to be some relationship between the shape of the premaxilla and that of the rostral scale. *Agkistrodon acutus*, for example, has a pointed rostral scale and a pointed premaxilla (fig. 16).

The shape of the premaxilla is variable within some species. In the various subspecies of *C. viridis* (fig. 15), the basal portion is usually pointed, but the dorsal process varies in thickness and shape.

Prefrontal. — The prefrontal (figs. 15, 16) of crotalids does not vary greatly within a species. In *Bothrops*, *Trimeresurus*, and *Lachesis*, it extends medially more than in *Agkistrodon*, *Crotalus*, and *Sistrurus*. The three posterior processes of the prefrontal are quite characteristic for each species with regard to relative size and fusion of processes (figs. 15, 16).

Vomer, turbinal, ethmoid. — These bones were not examined critically since their shapes and positions seemed not to vary greatly. The turbinals are relatively small in most species; however, they are large and have a high dorsal projection in the larger snakes, such as *C. ruber*, *C. atrox*, *C. adamanteus*, *C. durissus*, *B. atrox*, and *Lachesis muta*.

TABLE 7

Counts of tooth sockets in *Lachesis*, *Sistrurus*, and *Trimeresurus*, showing number of specimens, (range), and mean. See footnote in table 4.

Species	Palatine	Pterygoid	Dentary
L. muta	8(3)3	8(9-10)9.6	8(9-12)11
S. catenatus	17(1-3)2.6	19(5-7)6.5	20(9-10)9.1
S. miliarius	2(3)3	4(7-9)7.8	7(10-11)10.4
S. ravus	10(3)3	10(5-7)7.9	10(8-10)8.8
Sistrurus totals	29(1-3)3	33(5-9)6.4	37(8-11)9.4
T. albolabris	2(4)4	2(11)11	2(11-13)12
T. flaviviridis	4(0)0[1]	4(11-14)12.5	4(10-17)13.3
T. mucrosquamatus	——	——	2(10-11)10.5
T. puniceus	2(5)5	2(12)12	2(15-17)16
T. purpureomaculatus	2(4)4	4(8-12)10.8	4(11-12)11.8
T. stejnegeri	——	2(12-13)12.5	2(12-14)13
T. wagleri	9(5)5	10(13-14)13.5	8(11-16)14.5
Trimeresurus totals	19(0-5)3.6	24(8-14)12.1	24(10-17)11.6

[1]M. A. Smith (1943), quoting Walls, said that *T. jerdoni* also lacks palatine teeth.

Nasal. — The nasals of crotalids (figs. 17, 18) are paired flat bones, occasionally curved laterally and anteriorly, with ventrally projecting medial processes which meet, but do not fuse, at the midline. These processes articulate independently on the ventral surface of each frontal. There is usually a cartilage-like tissue connecting the anterior and lateral edges of the nasals with the premaxillae and prefrontals. The nasals are usually longer than wide.

The shape of the flat dorsal surface of the nasal (fig. 17) is variable within some species, such as *Crotalus durissus*, *C. horridus*, *C. mitchelli*, *C. molossus*, *C. viridis*, and *C. cerastes*. As noted above, some of this variation is geographic. Nasal variability in most species is so great as to eliminate the use of this bone in determining relationships.

Many species of crotalids have accessory hooks and processes on the lateral and posterior-lateral corners of the nasals (*e.g.*, *C. horridus* and *C. c. cerastes*, fig. 17). These processes are variable among the individuals within a species; for example, they were present on the nasals of only 3 of the 25 *C. cerastes* skulls examined. Possibly the variation results from differences in ossification during development. These processes are often destroyed or lost in preparation of skeletons.

One of the two skulls examined of the ridge-nosed rattlesnake, *C. willardi*, had the nasals slightly raised anteriorly.

Palatine. — The palatine (figs. 17, 18) is a thin, vertical tooth-bearing bone articulating with the anterior end of the pterygoid. It lies between, but does not articulate with, the medial wall of the maxilla and the lateral edge of the vomer. It is deeply imbedded in connective tissue and is dorsal to the ventral level of the maxilla. This position, plus its weak articulation to the pterygoid, probably reduces its effectiveness in food-holding during the swallowing of food.

In the supposedly primitive forms of the Crotalidae and in the Viperidae, the palatine is small and narrow. In each genus of the Crotalidae, it seems to have undergone similar evolutionary changes, becoming thin and high. It is high and triangular in most species of *Crotalus* and *Agkistrodon* (figs. 17, 18). There is often a small anterior process or knob on the palatine in advanced forms of these two genera. The palatine has a small dorsal process in *Lachesis*.
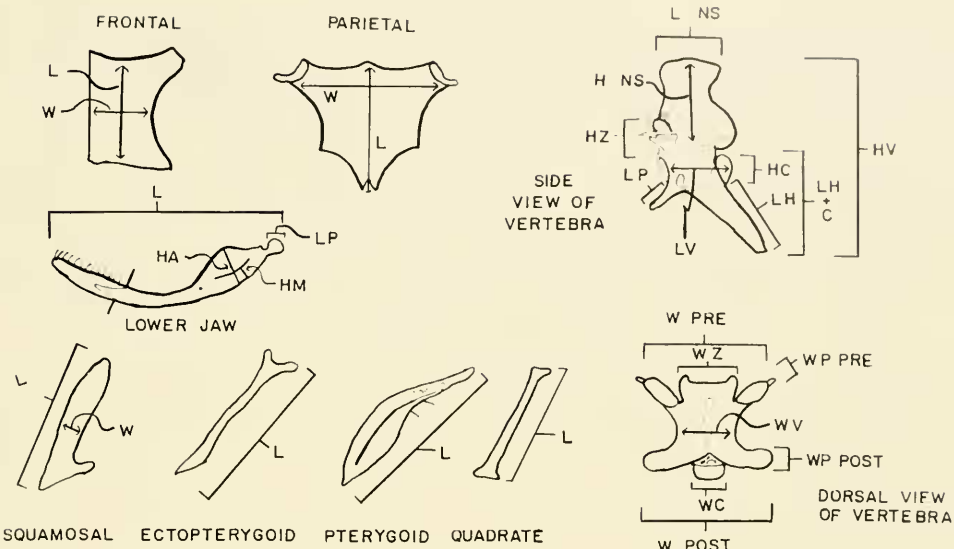
Fig. 3. Methods of measurement of crotalid bones.

Abbreviations: A, articular; C, centrum; H, height; L, length; LH, length of hypapophysis; M, Meckelian foramen lateral border; NS, neural spine; P, process; POST, postzygapophysis; PRE, prezygapophysis; V, vertebra; W, width; Z, zygosphene.

One of the more important characters that distinguish most species of *Bothrops* from *Trimeresurus* is that the palatine is forked in most of the former and in none of the latter (Ruiz, 1951). It is not forked in *B. nummifer* and *B. schlegeli*, two species that Ruiz did not examine.

Frontal. — The frontal bones (figs. 19, 20) are flat and elongate, square, or, occasionally, wider than long. They articulate posteriorly with the parietal and sometimes with the post-frontal, anteroventrally with the nasals, and anterolaterally with the prefrontals. The antero-lateral process has many shapes.

The lateral edge of the frontal lies above the eye socket and often is curved inward, conforming to the shape of the eye. Probably for the same reason, the frontal is often turned up laterally. In the sidewinder or horned rattlesnake, *Crotalus cerastes*, this raised portion supports the basal tissue of the horn. The horn itself is not, however, supported by bone, nor is it hard like that of the viperid *Cerastes cerastes* of the Sahara Desert. *Crotalus enyo* also has a raised frontal, where a small fleshy horn appears in life. The frontal of *Bothrops schlegeli* is flat and does not contribute to, nor seem to aid in, the support of the thin flap-like scale above the eye in that species. A raised frontal may contribute to the general shape of the head in other crotalids, aiding in support of the canthal ridge or supraocular scale.

The shape of the frontal is relatively constant in each species. The width of the bone was measured at its narrowest part, and the length was measured midway between the sides (fig. 3). The frontal is longer than wide in all species of *Bothrops* examined except *B. schlegeli* and *B. nummifer*. It is longer than wide in all species of *Sistrurus* and *Crotalus* except *C. adamanteus* and sometimes *C. atrox*. In *C. adamanteus* it is wider than long except in some very old specimens, in which it may measure longer than wide though it looks wider than long. The frontal of *C. atrox* is elongate in young individuals and in most adults, but a few large adults have frontals wider than long. The frontal is wider than long in *Lachesis muta* and *Trimeresurus wagleri*. The latter is the only crotalid with the center of each frontal depressed. All the other species of *Trimeresurus* have elongate frontals. The frontals of most species of *Agkistrodon* are elongate; those of *A. acutus*, *A. bilineatus*, and *A. piscivorus* are squarish and occasionally wider than long.

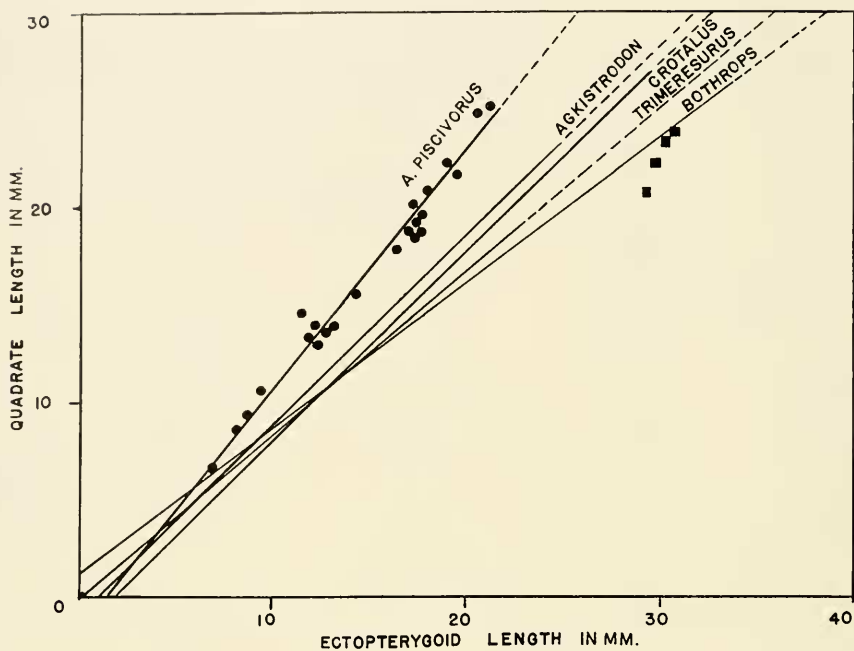Fig. 4. Relationship of quadrate length to ectopterygoid length in various crotalids. Solid line, observed range; dashed line, extrapolation; solid squares, *Lachesis*.
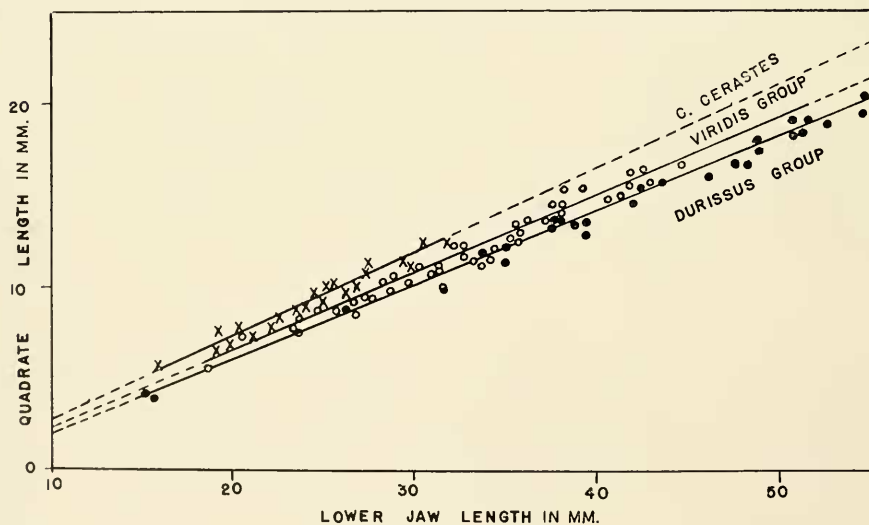

Fig. 5. Relationship of quadrate length to lower jaw length in a few species of *Crotalus*. Solid line, observed range; dashed line, extrapolation; solid circles, *durissus* group; open circles, *viridis* group; crosses, *C. cerastes*.

Maxilla (*Maxillary*). — The maxilla of crotalids (figs. 21, 22) is a heavy bone holding the functional fang. The maxilla has a large lateral opening which contains the heat-sensitive facial pit. Bullock and Cowles (1952) and Bullock and Fox (1957) discuss the anatomy and physiology of the facial pit and its relation to the shape of the cavity of the maxilla.

As described by Klauber (1939), the forward rotation of the fang is due to a change in position of the quadrate, forcing the ectopterygoid to push on the maxilla and to rotate it against the prefrontal. In *Crotalus* and *Sistrurus*, most of this forward rotation of the maxilla is afforded by the medial anterior process of the ectopterygoid, which lies flat against the posterior part of the maxilla. In *Bothrops* and *Agkistrodon*, the movement is due to the lateral process of the anterior end of the ectopterygoid pushing on the posterolateral corner of the maxilla. This articulation differs greatly in the various species of *Trimeresurus* (fig. 22).

The shape of the anterior edge of the pit cavity is of some taxonomic importance, as Ruiz (1951) has shown. This edge is a smooth open curve in *Agkistrodon* and *Bothrops* (fig. 22). In *Trimeresurus* it is irregular and may have a posteriorly pointing median process. This process is barely discernible in *Bothrops schlegeli;* it is absent in the related *B. nummifer.* The curvature of the anterior edge of the pit cavity of *Crotalus, Sistrurus,* and *Lachesis* has a definite, prominent posterior or dorsal process. In *Lachesis* this process has a small depression on its outer surface (fig. 22 and Ruiz, 1951). The prominence of this process is emphasized in *Crotalus* and *Sistrurus* (fig. 21) because of a depression posterior to the process. In some species (*C. viridis, tigris, mitchelli, cerastes, enyo,* and *scutulatus*) this depression extends anteriorly; this extension is one of the characters that suggest a close relationship among these species. The maxilla of *Trimeresurus* resembles the hypothetical primitive form of the family because of the relatively small size of the pit cavity.

Parietal. — The parietal (figs. 23, 24) is the largest and heaviest bone of the crotalid skull. It is a single bone that protects the brain and gives support and attachment for many of the head and jaw muscles.

The definitive shape of the parietal appears to be acquired during the first and second years of growth. In many species, however, there are changes throughout life in the shape and position of the lateral processes. The lateral processes are flat and thin and are parallel to the dorsal surface of the parietal, but more ventrally placed. The muscles of the lower jaw, the muscles of the squamosal-quadrate complex, and the muscles that force venom out of the poison gland are all attached to these processes. One, or part of one, of these processes usually forms a curved ridge at the anteromedial end of the squamosal. The medial limit of these processes is difficult to determine on young pit-vipers and on large adults of a few species. Because of the variability of shape and position of these processes, they were given little value in determining relationships. The term "dorsal surface of the parietal" is used in this paper for the shape of the dorsal surface excluding these lower lateral processes.

The shape of the dorsal surface of the parietal is characteristic for each species. It usually expands laterally just posterior to its anterior edge. The postfrontal bone articulates with the parietal on these lateral extensions. The greatest width of the parietal and of the skull is at this lateral extension; this width may be increased by the lateral extent of the postfrontal. The head width, as measured just posterior to the eye on preserved snakes, is equal to the greatest width of the parietal (or parietal plus postfrontal where the postfrontal extends beyond the parietal) plus the thickness of the skin. The anterolateral extensions of the parietal are often raised slightly, especially in those species in which the frontal is also raised.

Posterior to this lateral extension, the dorsal surface of the parietal narrows to a point or ridge, which is usually notched posteriorly. In some species there may be a second lateral expansion of the dorsal surface of the parietal (fig. 23, *C. atrox, horridus,* and *molossus*). The parietal extends posteriorly and laterally beyond the dorsal surface of the parietal and meets the occipital, squamosal, and otic areas.

In all crotalids the dorsal surface of the parietal is wider than long. It is T-shaped or triangular in *Agkistrodon.* It is squarish, trapezoidal, or triangular in *Bothrops,* except for
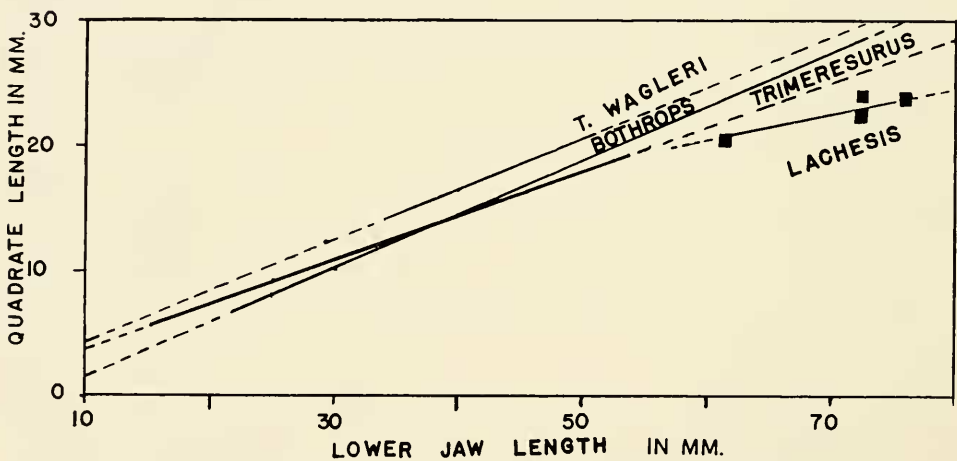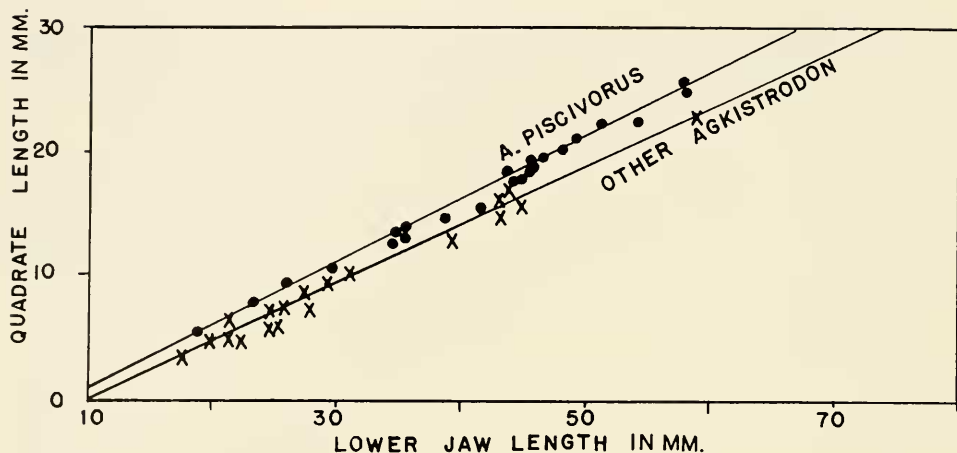
Fig. 6 (above). Relationship of quadrate length to lower jaw length in *Agkistrodon*. Solid line, observed range; dashed line, extrapolation; solid circles, *A. piscivorus*; crosses, other species of *Agkistrodon*.

Fig. 7 (below). Relationship of quadrate length to lower jaw length in a few genera of crotalids. Solid line, observed range; dashed line, extrapolation; solid squares, *Lachesis*.

B. nummifer and *B. schlegeli*, in which it is T-shaped. In *Lachesis* it is T-shaped, and in *Trimeresurus* it is elongately triangular or T-shaped. In *Crotalus* and in *Sistrurus ravus* the parietal is triangular. It is trapezoidal in *S. catenatus* and *S. miliarius*. In a small specimen of *S. catenatus tergeminus* (USNM 29132, Fort Davis, Texas) there is a small groove down the middle of the parietal. A similar groove was found on one specimen of *Agkistrodon contortrix*, a medium-sized adult from Kansas (UIMNH, no number).

The length of the dorsal surface of the parietal was measured at the mid-line, and the width was measured across the anterolateral extensions. On those species in which the post-frontal extends laterally beyond the parietal, two measurements were taken — parietal width and parietal width plus postfrontal. Because of the shape of the parietal under the postfrontal, the difference between the two measurements was not great except in *Lachesis*, in which the postfrontals extend laterally more than in any other crotalid.

A graph (not reproduced here) of length of the parietal plotted against width shows little variation for all crotalids. The curve for *Trimeresurus wagleri* and those for the "arboreal" group of *Bothrops* fall close together. The curves for *Trimeresurus* (other than *T. wagleri*) and those for the large terrestrial species of *Bothrops* also are close together. The curve for *Agkistrodon contortrix* is close to that for the Old World *Agkistrodon*, and the curve for *A. bilineatus* is closest to that for *A. piscivorus*. The curves for *Crotalus* and *Sistrurus* are closer to those for *Agkistrodon* than to those for *Bothrops* and *Trimeresurus*.

Postfrontal. — The postfrontal, though large and wide in the Viperidae, is very small in the Crotalidae. It appears to be undergoing a reduction in size within the family and is extremely small in *Bothrops nasuta*. Apparently, however, it is present in all crotalids though often lost in the preparation of the skull. Because of apparent loss, it is not shown on some of the drawings (figs. 23, 24).

The postfrontal is in a depression on the anterolateral expansion of the parietal and may articulate on the top, side, or end of this parietal extension. The postfrontal either touches the frontal or it does not. Which condition obtains is usually characeristic for a species, and in some groups it is useful in determining relationships. In some species, however, the condition is variable. In these species, the number of skeletons in which the postfrontal touches the frontal and the number in which it does not are as follows: *C. horridus*, 5-9; *C. mitchelli*, 1-9; *C. molossus*, 3-2; *C. ruber*, 10-4; *C. atrox*, 21-10; *B. neuwiedi*, 1-1; *A. bilineatus*, 5-1. In *C. ruber*, *C. atrox*, and *A. bilineatus*, the distance separating the two bones is always less than 1 mm.

Otic. — No great differences were noted in the otic areas of the skulls examined.

Occipitals. — The pit-viper skull contains a single supraoccipital, which is often fused with the parietal. The two exoccipitals (=lateral occipitals) meet on the mid-line dorsally and articulate with the basioccipital ventrally. The exoccipitals, together with the basioccipitals, form the foramen magnum and contribute to the occipital condyle. The basioccipital, which has a large ventral process, articulates with the basisphenoid and otic bones. The occipitals seem not to vary significantly in crotalids except for the basioccipital, which will be discussed below with the basisphenoid.

Stapes (*Columella auris*). — The stapes is a thin bone extending posteriorly and laterally from the oval window to the ventral side of the quadrate bone. Because the stapes is often lost in preparation, no special note was made of its variation.

It is often said that snakes "hear" by feeling vibrations from the ground (Tumarkin, 1955). Though no physiological or behavioral work has been done, it is suggested here that the stapes and its fusion to the quadrate might well act as a mechanism or route for transfer of sound to the inner ear. A vibration detected by the snake from the substrate might be transmitted by the lower jaw to the quadrate and then to the stapes, or by the ribs to the vertebrae, to the skull, to the quadrate, and to the stapes.

Basisphenoid. — The basisphenoid (figs. 25, 26) is a flat bone with a thin ventral process. This process fuses posteriorly with the ventral process of the basioccipital and separates the two muscle masses of the ventral surface of the skull. The basisphenoid and basioccipital form most of the ventral surface of the skull. The shapes of the anterior and anterolateral processes of the basisphenoid show individual variation that precludes the use of this character in determining relationships.

The ventral processes of the basioccipital and basisphenoid are shown in side view in figures 25 and 26. The ventral process of the basioccipital generally is heavy and curves posteriorly; it varies in curvature, height, and width. The ventral process of the basisphenoid is thinnest anteriorly. It becomes thick just before it joins the process of the basioccipital.

Members of the *atrox* group of *Crotalus* (*adamanteus*, *atrox*, *ruber*, and *tortugensis*) have a high ventral process on the basisphenoid. *Crotalus durissus* and *basiliscus* have a small anterior hump on this process. The members of the *viridis* group, except *C. mitchelli*, all have low ventral processes. Most of the small Mexican rattlesnakes (*C. lepidus*, *pricei*, and *tri-*
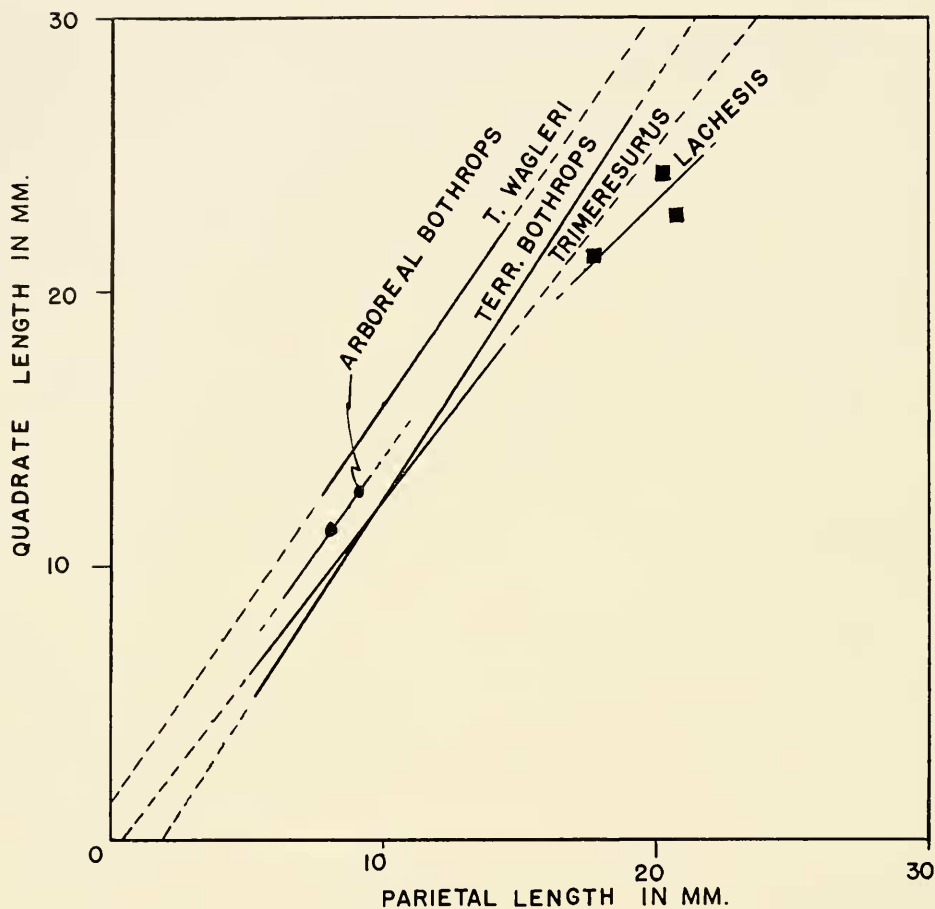
Fig. 8. Relationship of quadrate length to parietal length in a few genera of crotalids. Solid line, observed range; dashed line, extrapolation; solid squares, *Lachesis*.

seriatus) have low processes, as does *Sistrurus miliarius*. An anterior hump is characteristic of all *Agkistrodon* skulls examined. It is especially high and well developed in *A. acutus*, *bilineatus*, and *piscivorus*, and is small in all others, including *contortrix*. The anterior hump is present in the species of *Bothrops* except in *schlegeli*. *Lachesis muta* has a well developed rectangular process. The process is triangular in *Trimeresurus wagleri*. It is low in *T. albolabris*, *purpureomaculatus*, and *stejnegeri*, in the last having an anterior hump. *Trimeresurus puniceus* and *flavomaculatus* have well developed processes and anterior humps.

Squamosal. — The squamosal is a thin, flat bone lying on the posterolateral corner of the parietal. The anterior end of the quadrate lies on the dorsal surface of the posterior end of the squamosal. This junction is movable, but the motion is largely due to the action of the quadrate.

The squamosal varies in length and shape among the various pit vipers (figs. 27, 28). In *Crotalus* and *Sistrurus*, it has a lateral process or hook at its posterior end. The quadrate lies on the entire posterior end of the squamosal except for this process, which is round or pointed and forms an angle with the main part of the bone. This angle is 90° or less in *Crotalus*

basiliscus, horridus, lepidus, tortugensis, triseriatus, viridis, willardi, pusillus, and *Sistrurus cate-natus,* and usually (10 out of 11 specimens) in *S. miliarius.* The angle is so acute that it forms a hook in *C. pusillus, S. catenatus,* and *S. miliarius.* The hooked squamosal was used by W. E. Taylor (1895) to distinguish skulls of *Sistrurus* from those of *Crotalus.* However, the hook is lacking in *S. ravus* and is present in *C. pusillus;* thus this distinction does not hold.

Crotalus pricei has a squamosal unique among crotalids, with a peculiar posterior process. Furthermore, in one of the two specimens examined, the anterior end of the bone is forked, with several small processes or serrations between the arms of the fork (fig. 27), though in the other specimen the anterior end is flat.

In one skull examined (*Crotalus horridus,* LMK R-51), there are two squamosal bones on each side, one posterior and lateral to the other. The normal quadrate lies on the posterior squamosal, which lies on the anterior squamosal. The squamosals are abnormal in shape for this species, and it is probable that this condition developed during the healing of some injury.

Squamosal length was plotted against quadrate length for all species. The resulting graphs (not shown here) are a straight line for each species, with very little scatter. Lines of the species groups of *Crotalus* are close together. *Crotalus tortugensis* has a squamosal relatively shorter than that of *C. atrox.* This is one of the few characters in which this island species, related to *atrox,* extends beyond the scatter of *atrox. Sistrurus ravus* has a relatively short squamosal as compared to other species of *Sistrurus* and thus is similar to *C. lepidus* and *C. triseriatus.* The slopes of the curves are distinct for *Bothrops, Trimeresurus, Lachesis,* and *Agkistrodon.* The greatest divergence from the family norm is found in *Lachesis,* which has a squamosal relatively longer than that of the other genera. *Trimeresurus wagleri* and *T. puniceus* differ greatly from most species of *Trimeresurus* in having relatively small squamosals and large quadrates. This condition is found also in *Bothrops schlegeli,* but not in *B. nummifer.*

Quadrate. — The quadrate does not vary greatly in shape among the crotalids examined. It is usually wide anteriorly, narrowing posteriorly until just before the posterior articulation, where it expands. This articulation is wide, smooth, and often forked. No generic or major specific differences in shape were noted.

The quadrate bone is of different relative length in different crotalids. In was hoped that the differences in length could be associated with a possible increase in efficiency in fang rotation. From a physical model and from mathematical calculations, Dr. Blaine H. Levedahl has suggested (personal communication) that any increase in relative length of any of the segments in the fang rotation sequence (skull, quadrate, pterygoid, ectopterygoid) would increase the mechanical efficiency of the system. An equal proportional increase in all parts would not increase the efficiency, but an increase in length of one part would. If this is the case, the relatively large ratio of squamosal to quadrate in *Lachesis* would make the bushmaster the most efficient in this regard. The primitive *Trimeresurus wagleri,* with its relatively short squamosal, would probably be the most inefficient. The quadrate is relatively short in *Lachesis* and relatively long in *T. wagleri,* however.

Graphs of squamosal length plotted against quadrate length have already been discussed. Pterygoid length plotted against quadrate length also resulted in straight-line graphs with almost no scatter. Specific and generic differences can be noted but are not great.

Graphs of ectopterygoid length versus quadrate length are similar — they are straight lines with slight scatter. Generic and specific differences are noticeable (fig. 4). In *Agkistrodon piscivorus,* the quadrate is longer than the ectopterygoid. In other crotalids, it is usually shorter; the only exceptions seen are one specimen of *Crotalus scutulatus* and a few very large individuals of *C. atrox* and *C. adamanteus.* Measurements for *A. contortrix* fall on the same general line as those of the Old World species of *Agkistrodon.* The line for *A. bilineatus* is intermediate between those for the Old World *Agkistrodon* and *A. piscivorus* (fig. 4). The latter two lines have very little scatter.

Quadrate length plotted against lower jaw length also gives straight lines, with almost no scatter. Specific differences in ratios are difficult to discern, but generic and subgeneric lines are distinct. A few of these graphs are shown in figures 5 to 7.

Graphs of quadrate length against parietal length also are straight lines, though the scatter is great. The quadrate is always longer than the parietal. In *T. wagleri* the quadrate is relatively longer than that in most species of *Trimeresurus*. A relatively elongate quadrate is found also in *B. schlegeli* and *B. nummifer*. Except for these three species, the lines for *Bothrops* are different from those for *Trimeresurus* (fig. 8). No other major differences are noticeable.

Pterygoid. — The pterygoid (figs. 29, 30) is a toothed bone that is narrow anteriorly, where the teeth are present, and thin and flat posteriorly. Anteriorly, the pterygoid articulates with the palatine, and posteriorly it joins with the articular bone. The pterygoid is curved laterally in its middle third. The curvature on the lateral edge of the bone is more anterior than that on the medial edge. The ectopterygoid usually fits into a groove on the lateral edge of the pterygoid and may articulate anterior to, in the middle of, or posterior to the lateral curvature (figs. 29, 30).

In *Crotalus*, *Sistrurus*, and *Lachesis*, the pterygoid teeth extend at most only to the middle of the junction with the ectopterygoid and often not so far. In the other genera of crotalids and in the viperids, the teeth extend beyond this junction.

The posterior part of the pterygoid usually has a ridge on its ventrolateral surface. This ridge may be bordered by deep lateral grooves. Occasionally the top of this ridge is bent over laterally and thus encloses a small cavity. Many muscles attach on the ventral surface of the pterygoid, and the shape and position of the ridge are often related to the position of attachment of these muscles. An additional ventral process is present on the pterygoid of *Agkistrodon acutus* at the ectopterygoid junction.

The shape of the posterior portion of the pterygoid, the curvature of the medial and lateral edges, the position of the ectopterygoid junction, and the size and shape of the ridge on the ventral surface of the pterygoid, all are quite characteristic of each species (figs. 29 and 30). These characters are, however, difficult to classify or describe and thus are difficult to use in determining relationships.

Pterygoid-quadrate graphs have been discussed. A graph of pterygoid length against ectopterygoid length is shown in figure 9. Generic differences are apparent. *Trimeresurus wagleri* conforms in this character with the rest of the genus. The lines for *Sistrurus* and *Crotalus* appear different when extrapolated. The range (solid line) of *Sistrurus*, however, conforms closely with the range (solid line) of *Crotalus* and falls within its scatter. The measurements for *Agkistrodon contortrix* fall within the scatter of the Old World *Agkistrodon* line. The line for *A. piscivorus* is distinct but close to that for *A. bilineatus*. The number of specimens available of *Lachesis* and arboreal species of *Bothrops* was too small to permit drawing any curves.

Graphs of pterygoid length potted against lower jaw length show no specific or generic differences. All measurements of all species fall very close to a single line.

Ectopterygoid (External pterygoid, transpalatine, transverse, transverse pterygoid). — The ectopterygoid is a flat, thin bone extending from about the middle of the pterygoid, passing under the eye, and articulating with one or more points on the posterior wall of the maxilla. The ectopterygoid is usually forked anteriorly. In a few species the shape of this fork shows individual and ontogenetic variation, but in others the shape is quite diagnostic and is useful in determining relationships (figs. 29, 30).

The lateral process of the fork of the ectopterygoid is quite round in *Crotalus ruber*, and this process turns ventrally in *C. tortugensis*. *Crotalus triseriatus* has a thin lateral flap on its ectopterygoid. The primitive shape of this bone is probably broad and flat, with a wide anterior end. This condition is seen in some Viperidae and in *Trimeresurus wagleri, purpureomaculatus, albolabris, stejnegeri,* and *Bothrops schlegeli* (figs. 29, 30).

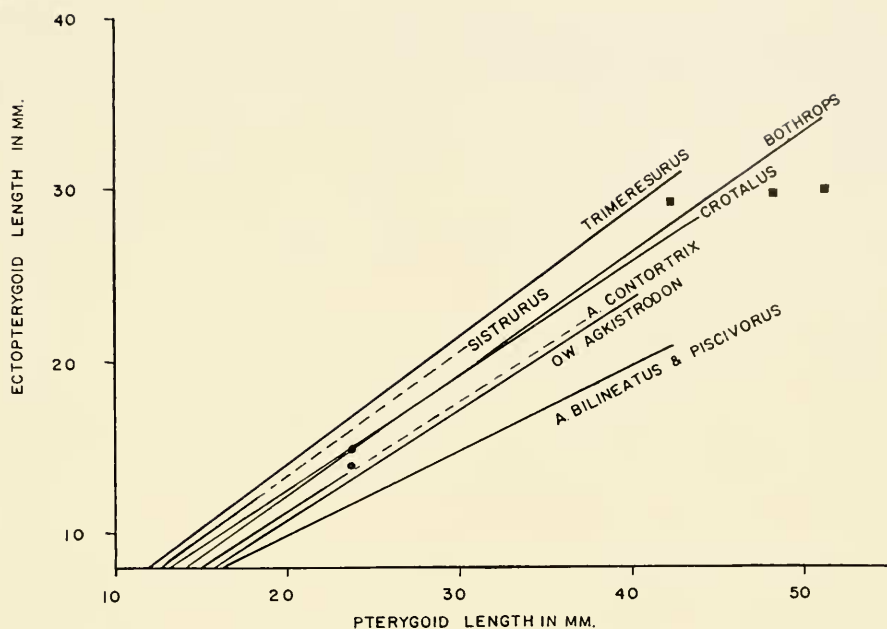Fig. 9. Relationship of ectopterygoid length to pterygoid length in the crotalids. Solid line, observed range; dashed line, extrapolation; dots, arboreal group of *Bothrops;* solid squares, *Lachesis.*
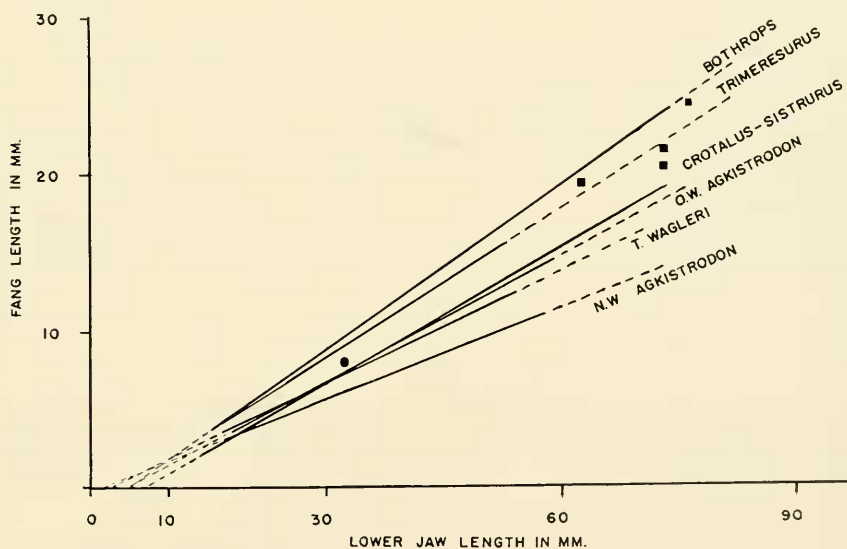

Fig. 10. Relationship of fang length to lower jaw length in the crotalids. Solid line, observed range; dashed line, extrapolation; dot, arboreal group of *Bothrops;* solid squares, *Lachesis.*

The posterior part of the ectopterygoid generally is narrower than the anterior part and usually is flat or twisted. The junction of the ectopterygoid with the pterygoid is either flat, in a groove in the pterygoid, or supported by lateral flaps of the ectopterygoid. The junction of the ectopterygoid with the pterygoid is usually characteristic for each species. The curvature, twisting, and posterior articulations of the ectopterygoid are difficult to interpret in terms of relationships. The shape of the anterior end of the bone is more useful in this regard.

The ectopterygoid is shorter than the basal portion of the pterygoid in all species of *Agkistrodon* except *acutus* and *strauchi*; thus this character cannot be used to distinguish all species of *Agkistrodon* from other crotalids as Ruiz (1951) and W. E. Taylor (1895) proposed.

Graphs of ectopterygoid length against lower jaw length show few distinctions except on the generic and subgeneric levels.

Lower Jaw. — The lower jaw of crotalids (figs. 31, 32) contains four bones, the articular, angular (e), dentary, and splenial. The coronoid bone is absent in crotalids, as in most other snakes. Both angular and splenial are small and lie on the medial side of the lower jaw. The shape and relationship of these two bones and their position in regard to the internal Meckelian foramen are of some taxonomic importance.

The tooth-bearing dentary bone is usually blunt anteriorly and is joined to the dentary of the opposite side by a ligament at the mid-line. The dentary has two posterior processes, a dorsal and a ventral, which fit above and below an elongate process of the articular. The splenial and angular lie medial to this junction. This dentary-articular junction is probably the weakest point in the crotalid skull, to judge from the frequency with which it is broken. The teeth on the dentary extend almost to the posterior tip of the dorsal surface of the dorsal process. The lower process of the dentary extends farther posteriorly than does the dorsal, except in a few species (*A. hypnale, A. piscivorus, B. bilineatus, B. jararaca, B. schlegeli,* figs. 31, 32; tables 10 and 12). The two processes are equal in length in *A. acutus,* in *B. atrox,* and in *T. wagleri.*

The dentary has a small mental foramen on its external surface, the position and shape of which do not appear to be taxonomically significant.

The articular is the longest bone in the lower jaw and probably represents the fused articular, prearticular, and surangular (Gilmore, 1938; Williston, 1925). The posterior portion of the articular meets the quadrate in a dorsal saddle-shaped articulating surface. Posterior to this junction there is a heavy process which curves inward. The pterygoid articulates with the U-shaped area formed by this process. The ventral curvature of the articular appears to be a character of no taxonomic value, changing somewhat with growth. The articular may have a thin flap or process on its ventrolateral edge just below the point of articulation of the quadrate, as in *Trimeresurus wagleri* and *Crotalus atrox, mitchelli, molossus, ruber,* and *viridis* (figs. 31, 32). This appears to be a specific characteristic in some species and a variable character in others (*e.g., C. ruber* and *viridis*).

The posterior part of the articular has a thin high medial hump probably representing the embryonic surangular. This hump lies just anterior to the junction of the quadrate, and it forms the medial wall of the large posterior Meckelian foramen. The shape of this hump is characteristic for each species, but the differences are those of slight changes in curvature and hence are difficult to interpret for use in determining relationships.

The posterior Meckelian foramen is open dorsally and laterally. Ventrolaterally, it is bordered by another part of the articular. The extent and shape of the opening of the foramen are specific characters. There seem to be trends in several phyletic lines of crotalids towards increase in the size of this opening and trends in other groups toward a reduction in its size.

There is a small foramen in the lateral wall of the articular. This foramen is usually on the long, narrow part of the articular, but in some species (*e.g.*, most species of *Trimeresurus*, *B. schlegeli*, *C. intermedius*; figs. 31, 32) it occurs within or below the area of the posterior dorsal hump.
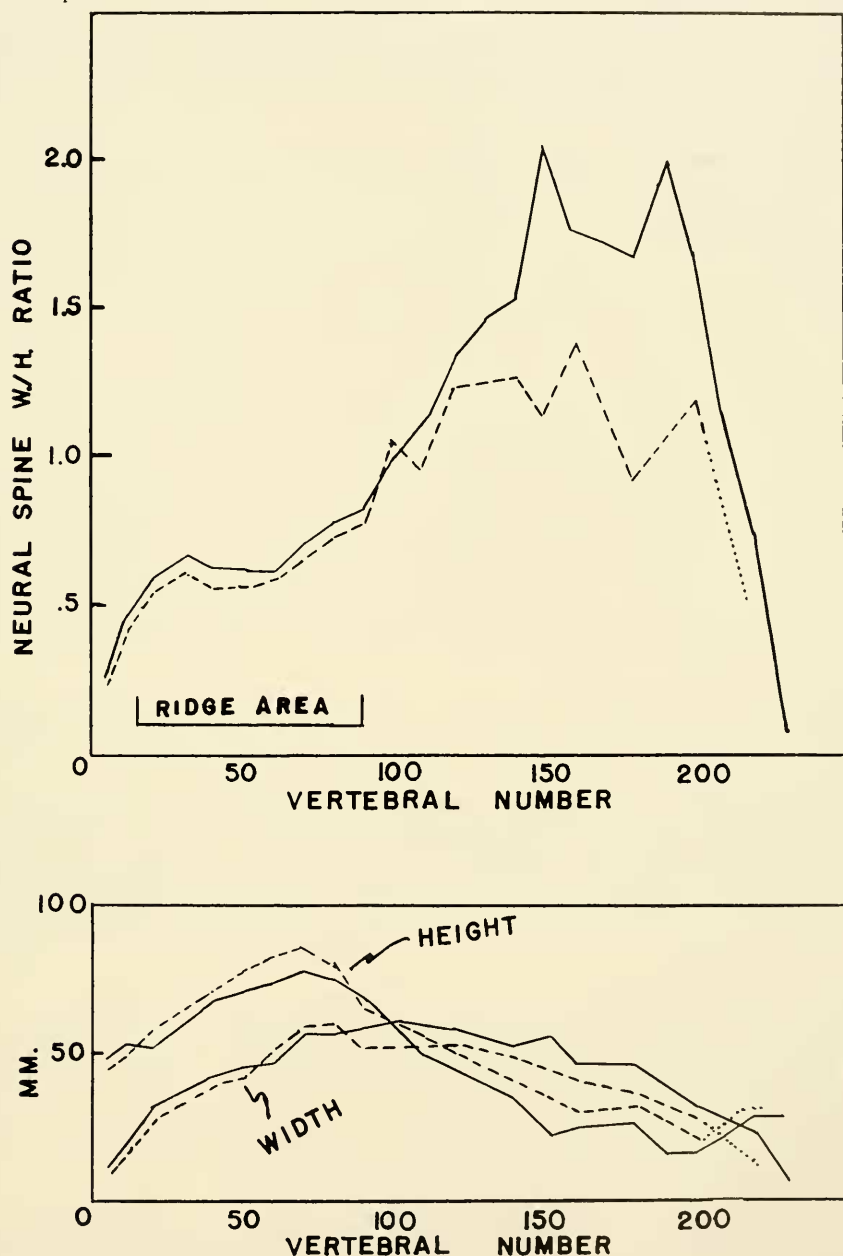

Fig. 11. Relationship of size of neural spine to position within the vertebral column in two specimens of *Crotalus durissus tzabcan* (MVZ 45726 and 45727) from Yucatán.

Figure 10 is a graph of lower jaw length plotted against fang length. The lines for *Bothrops* and *Trimeresurus* are separate. The lines for *T. wagleri* and *B. schlegeli* differ from those for the other members of their respective genera. This is one of the few characters in which the Old World and New World species of *Agkistrodon* are different. With very little scatter, the measurements for *A. contortrix*, *A. bilineatus*, and *A. piscivorus* all approximate a single line. The *Crotalus* and *Sistrurus* lines are indistinguishable. The few measurements of *S. ravus* suggest a possible ontogenetic allomorphic change for these characters during growth. Nothing significant is revealed in graphs of measurements of several other characters of the lower jaw.

Vertebrae. — A typical crotalid vertebra was described and figured by Klauber (1956) and is shown here in figure 2. The thoracic vertebrae of the Crotalidae each have a long hypapophysis projecting ventrally from the centrum. The diapophyses are small tubercles. A small process extends anterior and ventral to the diapophysis. It is probably part of the diapophysis and is termed the parapophysis (Simpson, 1933; Brattstrom, 1954). The first two vertebrae are relatively simple, with the first lacking a neural spine. The hypapophysis divides into two distinct and separated parts posterior to the sacrum. These parts are called lymphapophyses.

In general, the vertebrae of all the crotalids are similar, differing only in minor shapes and proportions. For example, the midthoracic vertebrae of *Bothrops* and *Trimeresurus* each have a well developed ridge extending from the posterolateral corner of the zygosphene to the posterior edge of the articulating surface of the prezygapophysis. This ridge is absent in the other genera. In *Bothrops* and *Trimeresurus* and in a few species of *Agkistrodon*, the lateral process of the prezygapophysis usually does not extend more than 1 millimeter beyond the articulating surface. There is a triangular depression on the anterior face of the prezygapophysis in *Agkistrodon*. This depression is lacking in *Crotalus* and *Sistrurus* except for the area immediately around the foramen and lateral to the centrum cup. There is a groove in the posterior edge of the neural spine in most species of *Crotalus*. This groove is usually absent in *Sistrurus catenatus* and *miliarius* or, if present, extends only halfway up the neural spine; vertebrae of *S. ravus* were not seen.

The above-mentioned generic differences are relatively constant in most species, but they are not always valid in specialized or primitive species or in young individuals. It is important, however, to be able to identify the various species of crotalids by the vertebrae since they are the most common elements found in fossil deposits. Numerous subtle differences can be used to distinguish between the vertebrae of the different species, but these are often difficult to describe. The situation is complicated further by the fact that there are relative and proportional size differences among the vertebrae of a single individual. For example, the neural spine is tall and narrow on the anterior vertebrae of most crotalids. It increases in height in the first 50 to 80 vertebrae and then decreases (fig. 11). At the point of maximum height, the neural spine is still increasing in width. Similar changes within the vertebral column can be noted for other characters (fig. 12).

Several methods could be used for a quantitative differentiation between the vertebrae of different species of crotalids. One specific vertebra could be used as a standard for a species (*e.g.*, vertebra number 80 or number 100). In fossil deposits, however, the vertebrae are usually separated, and it is impossible to determine which vertebra is number 80 or 100. A more useful standard would be to use the vertebra which has, for example, the neural spine height equal to the neural spine width. Fragmentation and weathering in fossils would require that several criteria be used.

Where large series of vertebrae are available, it is sometimes useful to use ratio diagrams on a log-difference scale of a series of analogous measurements, comparing a sample with a known standard. This method, developed by Simpson (1941), was used by Brattstrom (1954) in distinguishing Pleistocene and Recent crotalids of Florida. Vertebrae can also be distinguished by the use of simple proportions and ratios (Johnson, 1955b); see table 8.

TABLE 8

Ratios of measurements of mid-thoracic vertebrae.

Species	$\frac{W\ Post[1]}{H\ NS}$	$\frac{HV[2]}{H\ NS}$	$\frac{HV[3]}{W\ Post}$
C. adamanteus	1.82	2.76	1.52
C. atrox	1.69	2.72	1.60
C. basiliscus	2.31	3.71	1.61
C. cerastes	2.16	2.84	1.31
C. durissus tzabcan	1.41	2.42	1.72
C. enyo	1.26	2.26	1.79
C. lepidus	2.37	3.00	1.26
C. mitchelli	2.38	2.46	1.03
C. molossus	2.22	—	—
C. pricei	3.05	3.95	1.29
C. ruber	2.23	2.99	1.34
C. scutulatus	2.17	3.10	1.43
C. tigris	1.68	2.81	1.67
C. v. concolor	2.85	3.39	1.19
C. v. viridis	2.90	3.50	1.21
C. willardi	3.75	3.66	0.97
S. catenatus	1.93	2.96	1.53
S. miliarius	2.70	3.80	1.41
A. contortrix	1.85	2.90	1.57
A. piscivorus	1.54	2.32	1.51

[1]Width across postzygapophyses/height of neural spine.
[2]Height of vertebra/height of neural spine.
[3]Height of vertebra/width across postzygapophyses.

Since differences occur along the vertebral column of a single snake, it was decided to graph measurements of every 10th or 20th vertebra for the length of the vertebral column. This was first done with two specimens of *Crotalus durissus*, using two characters (fig. 11), and then with a skeleton of *Crotalus ruber*, using several characters (fig. 12). The two graphs show the kinds of changes within the vertebral column of one snake but do not permit species comparisons because of size differences.

To compare species, ratios of the various characters to height of the vertebrae were computed and graphed for *C. ruber* and *durissus* (figs. 13, 14) and for some 15 other species of crotalids. The position and crossing of the various lines seem to be characteristic for each species. These graphs also can be used for identifying vertebrae. For an unidentified vertebra, first the ratios of the measurements to the height of the vertebra are plotted on a card with the same scale as the graph. The card is then moved across each graph until a point is found where all the lines on the card conform with the lines on the graph. Conformity should occur at only one position on only one graph, thus indicating the serial position and the species of the unknown vertebra. This technique has proved successful, but, of course, it works only with species for which graphs are available. Furthermore, these graphs fail to show such important details as the curvature and shape of parts, which are characters of some importance in species determination.
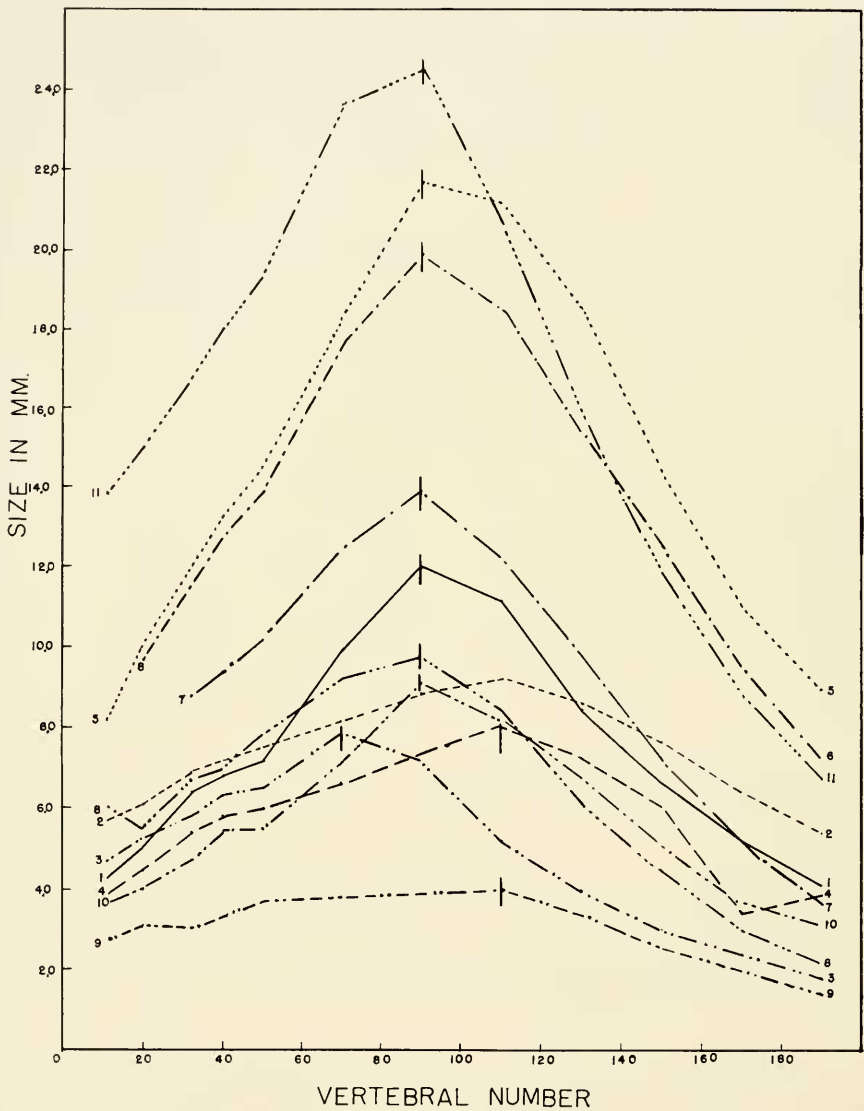
Fig. 12. Relationship of several characters to position within the vertebral column in one specimen of *Crotalus ruber ruber* (BHB 1628).

Characters: 1, width of vertebra; 2, length of vertebra; 3, height of neural spine; 4, length of neural spine; 5, width across prezygapophyses; 6, width across postzygapophyses; 7, hypapophysis length including centrum; 8, hypapophysis length; 9, height of zygosphene; 10, width of zygosphene; 11, height of vertebra.

Fig. 13. Relationship of characters to position within the vertebral column (expressed as ratios of vertebral height) in one specimen of *Crotalus ruber ruber* (BHB 1628). Characters as in figure 12.
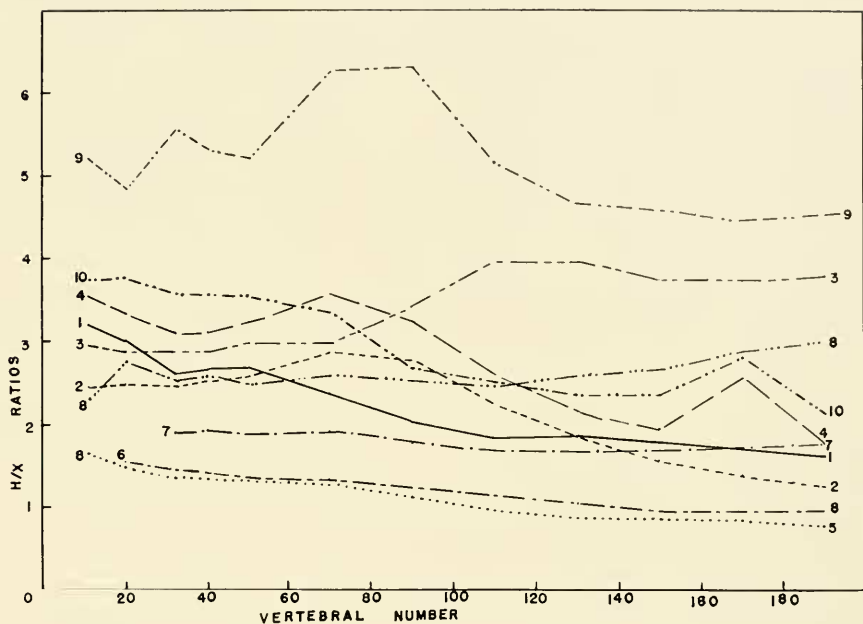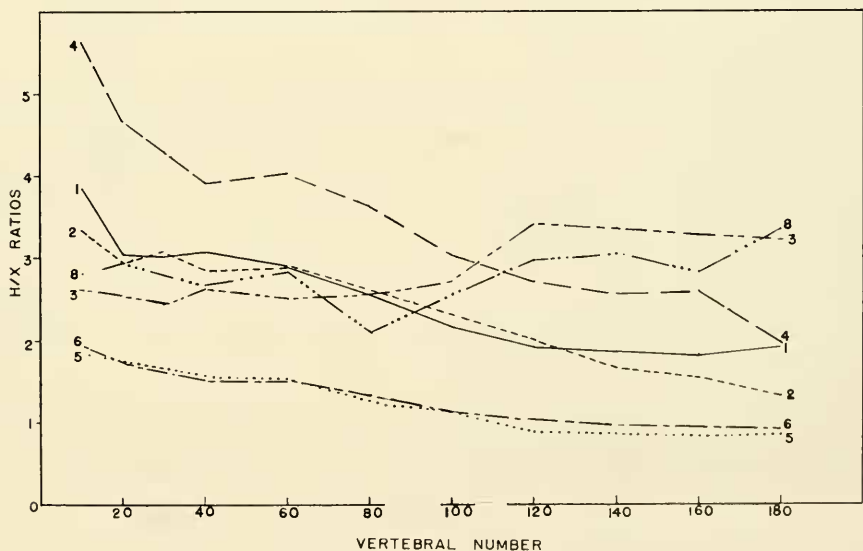

Fig. 14. Relationship of characters to position within the vertebral column (expressed as ratios of vertebral height) in one specimen of *Crotalus durissus tzabcan* (MVZ 45726). Characters as in figure 12.

TABLE 9

Length/width[1] ratios of midthoracic ribs.

Species	Ratio	Species	Ratio	Species	Ratio
A. bilineatus	3.33	C. cerastes	3.46	C. scutulatus	3.10
A. contortrix	3.88	C. cerastes	3.51	C. viridis helleri	3.98
A. contortrix	3.61	C. durissus tzabcan	3.52	C. viridis helleri	4.65
A. piscivorus	3.57	C. durissus tzabcan	3.20	C. viridis lutosus	5.08
C. atrox	3.66	C. horridus	3.68	S. catenatus	3.78
C. basiliscus	2.18	C. mitchelli pyrrhus	3.19		

[1]Width is depth of curvature, *i.e.*, the maximum distance from the central part of the rib to the line connecting the ends.

Measurements of crotalid vertebrae are taken in essentially the same manner as described by Johnson (1955b) or as shown in figure 3. A few measursements, however, need further elaboration.

Height of vertebra. — Greatest height of the vertebra (HV), measured from the top of the neural spine to the tip of the hypapophysis, with the calipers flat along the top of the neural spine.

Width of vertebra. — Width of the vertebra (WV) at its narrowest point between the prezygapophyses and the postzygapophyses.

Length of vertebra. — Length of the centrum, from the center of the cup anteriorly to the center of the ball posteriorly (LV).

Width across prezygapophyses. — Greatest width across the prezygapophyses (W Pre. Z), including the tip of the process.

Width of process of prezygapophysis. — Anteroposterior width of the articulating surface (= process) of the prezygapophysis (W P Pre). (Not the width of the small lateral process measured in "width across prezygapophyses.")

Width across postzygapophyses. — Greatest width across the postzygapophyses (W Post).

Width of process of postzygapophysis. — Anteroposterior width of the articulating surface of the postzygapophysis (W P Post).

Centrum length. — See length of vertebra.

Centrum height and width. — Height and width of the ball of the centrum (HC and WC).

Neural spine height. — Height of the neural spine measured from the base of the neural spine (= zygosphene-zygantrum ridge) to the top of the spine at a point about half-way between its anterior and posterior edges (H NS). The height of the neural spine as measured at the zygosphene or at the zygantrum is often unreliable because of the variation in thicknesses of the zygantrum and zygosphene.

Neural spine length. — Anteroposterior length of the neural spine at the top of the spine (L NS). (Erroneously referred to as "neural spine width" by Brattstrom, 1953, 1954.)

Zygosphene height. — Height measured from the dorsal edge of the cup of the centrum to the top or shelf part of the zygosphene (HZ).

Width of process of zygosphene. — Anteroposterior width of one side (= process) of the zygosphene (WZ).

Hypapophysis length. — Measured in two ways: first, from the top of the ball of the centrum to the ventral tip of the hypapophysis (LH); second, from the ventral base of the ball of the centrum to the tip of the hypapophysis (LH + C). The second measurement is distinguished by the term "including centrum."

Hypapophysis width. — Anteroposterior width of the middle of the hypapophysis (unless mentioned otherwise, *e.g.*, *Crotalus giganteus*, Brattstrom, 1954).

Parapophysis length. — Length of parapophysis (LP) from the base (junction with the anterior face of the prezygapophysis) to the tip.

Parapophysis width. — Width (from side to side) at the middle of the parapophysis (WP).

Ribs. — Ribs are found on all the presacral vertebrae of crotalids except the first two (atlas and axis). The first sacral rib is forked distally, with the ventral process longer than the dorsal. The second sacral rib is forked to the base. The third sacral rib has the dorsal part completely separate from the ventral. The dorsal part is apparently immovably articulated and
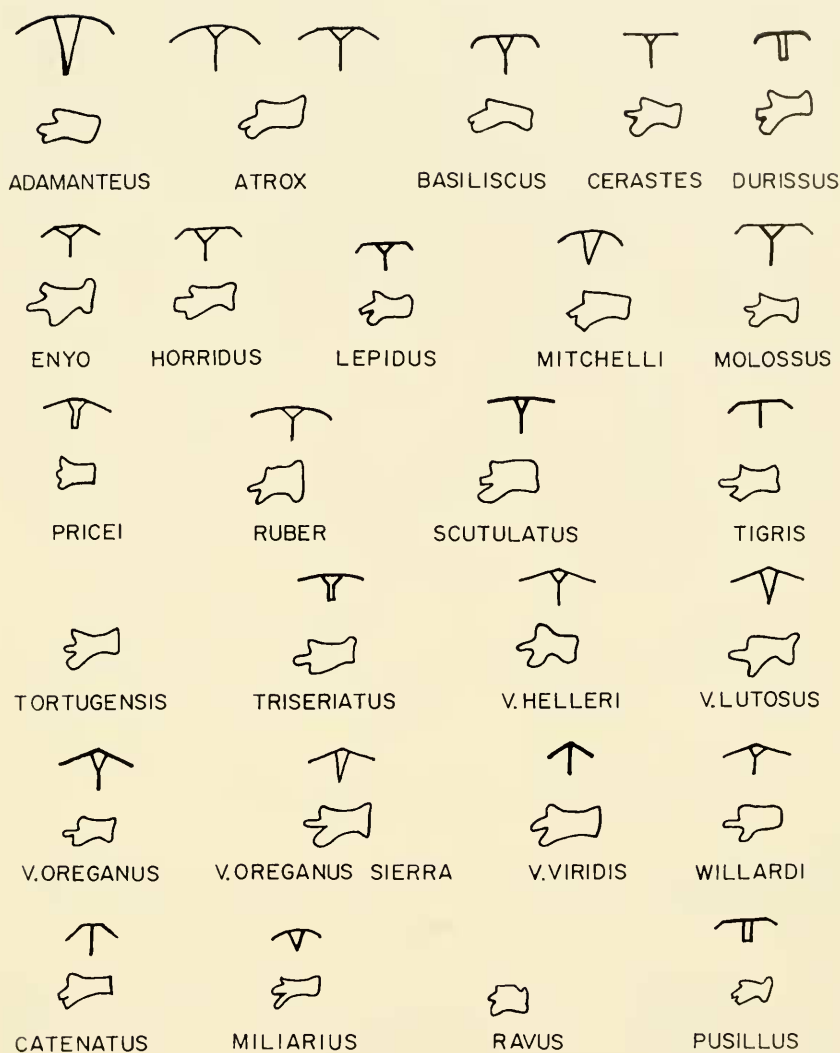
Fig. 15. Premaxillae and prefrontals of species of *Crotalus* and *Sistrurus*.

the ventral movably articulated to the vertebra. In each of the next two vertebrae, evidently the first and second caudal vertebrae, both the dorsal and ventral processes are fused to the vertebra. In the third and fourth caudal vertebra, these processes are fused to each other. On each succeeding caudal vertebra they remain as thin, narrow, immovable lateral processes. These processes may serve as attachments for cloacal and scent-gland muscles.

A typical crotalid rib is thin and elongate, with two dorsal heads. No major differences were noted in the articulating surfaces of the ribs in any of the crotalids. Some individuals seemed to have heavier heads on the ribs than others, but this condition is usually associated with the large size of the snake.
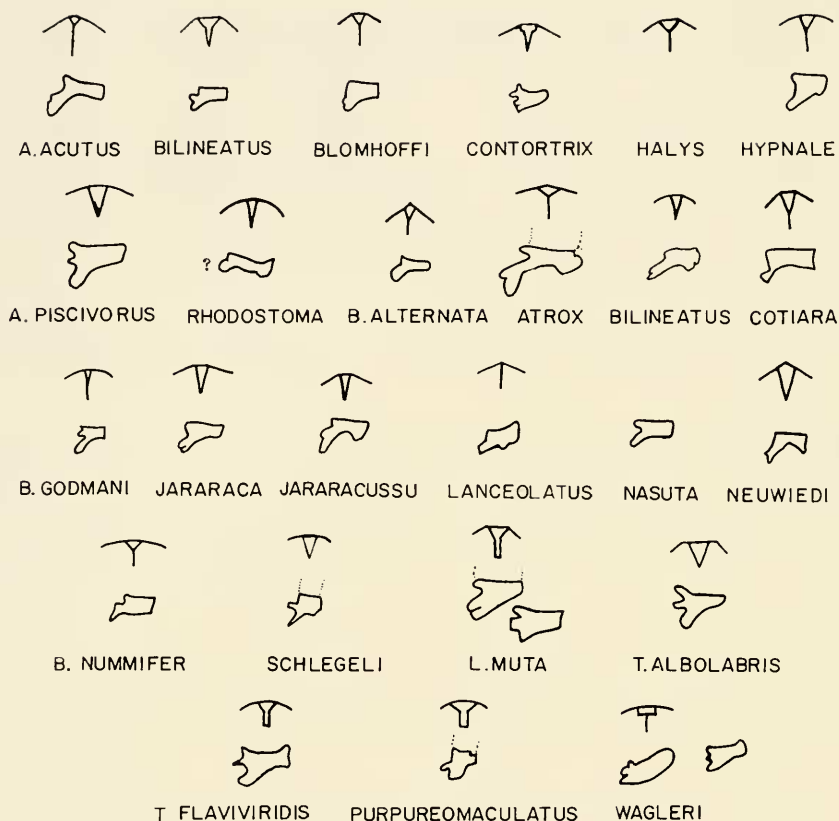
Fig. 16. Premaxillae and prefrontals of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*.

Ribs vary in length and curvature within one snake. The curvature of the mid-thoracic ribs often reveals (or results from) the general habitus of the snake; for example, *Crotalus durissus*, with a high body, has long ribs with slight curvature, whereas *C. basiliscus*, with a low, flat body, has more curvature to the ribs. Length-width ratios of midthoracic ribs of a few crotalids are presented in table 9. Width in this case means curvature (= depth of arc) and is measured from the lateral curvature of the rib to a line connecting the ends. Some differences between the ribs of several species (*e.g.*, *C. basiliscus* and *durissus*, as just mentioned) can be seen from table 9, but also note the variation in two specimens of *durissus* and in two specimens of *C. v. helleri*. Ribs were not used as a taxonomic character in determining relationships because of their ontogenetic, serial, and individual variation.

Shaker. — The shaker or style of the rattlesnakes, *Crotalus* and *Sistrurus*, represents the fused terminal 9th to 11th caudal vertebrae. The muscles that vibrate the rattle are inserted on the base of the style. The anatomy of the shaker was described by Klauber (1940, 1956) and by Zimmermann and Pope (1948).

No major differences could be found in the shaker of the various species of rattlesnakes examined, and no differences could be found to distinguish the shakers of *Crotalus* and
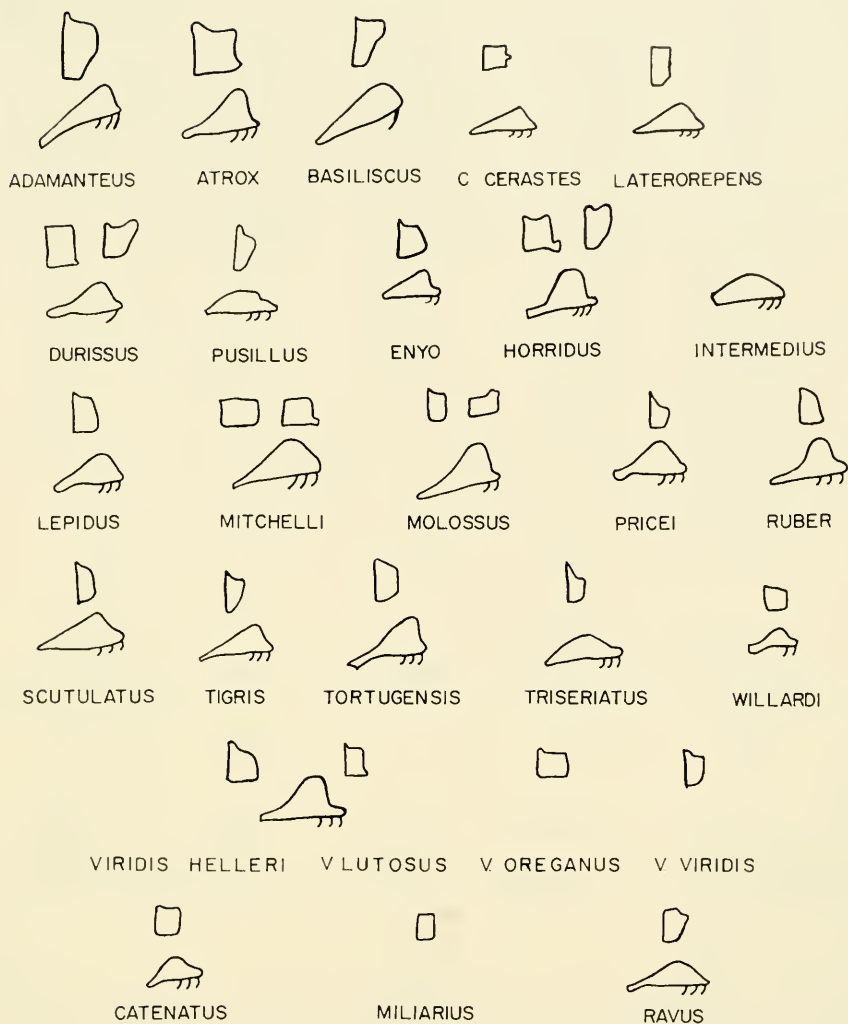
Fig. 17. Nasals and palatines of species of *Crotalus* and *Sistrurus*.

Sistrurus except for the temporal difference noted by Zimmerman and Pope (1948). Length of the shaker was plotted against width and against height. There were no consistent differences or similarities among the various species. The variation in one species was often as great as the entire range for the two genera. There was a general increase in size of the shaker with increase in size of the snake, but with no consistency in ratio. The variability found is probably related to the fact that the shaker represents many centers of ossification plus extravertebral additions. There may be differences in the number of vertebrae in the shakers of various species, but because of the method of development and the fusion of parts, the number is almost impossible to determine.
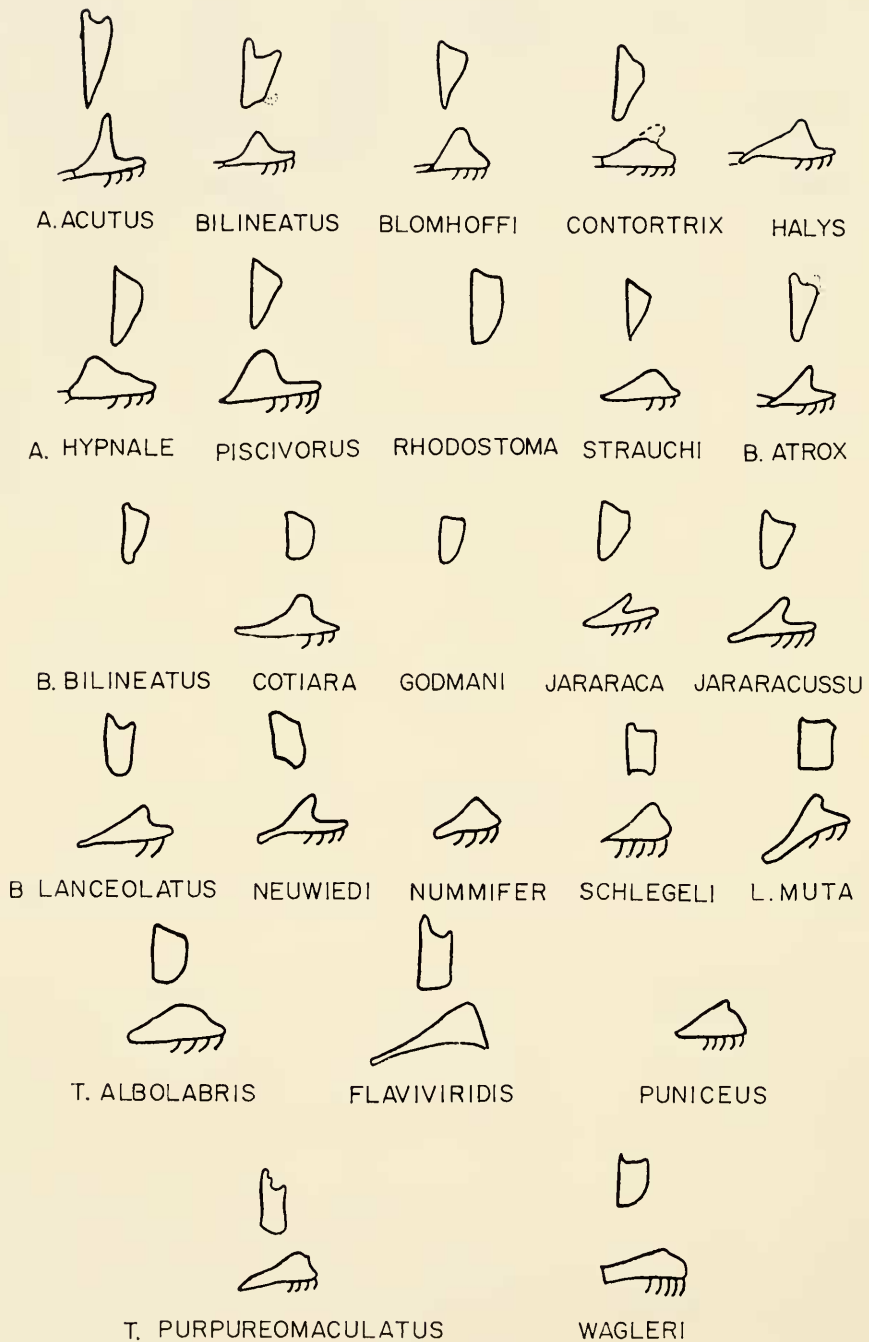
Fig. 18. Nasals and palatines of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*.
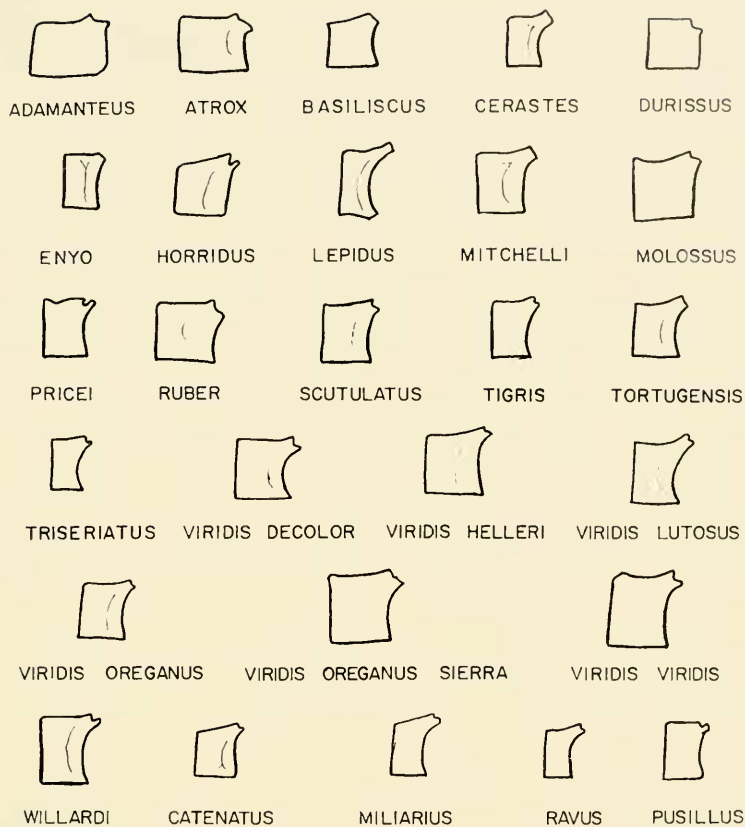
Fig. 19. Frontals of species of *Crotalus* and *Sistrurus*.

PHYLOGENY

Several workers have suggested phylogenies for the Crotalidae. Among the first of these was Garman (1889). Recent contributions to knowledge of relationships within the family were made by Amaral (1929), Githens and Butz (1929), Githens and George (1931), Githens (1935), Mosauer (1932, 1935), Maslin (1942), and Minton (1956). Phylogenetic trees were presented for *Crotalus* and *Sistrurus* by Amaral (1929), Githens and George (1931), Gloyd (1940), H. M. Smith (1946), and Klauber (1956).

Fossil crotalids contribute little to our knowledge of relationships within the family. A detailed report on the fossil crotalids was made by Brattstrom (1954) and summarized by Klauber (1956).

Except for scutellation, non-osteological data are lacking or contribute little to our knowledge of relationships within the family. Data concerning the biochemistry and physiological action of crotalid venoms (Minton, 1956) contribute supportive evidence for some relationships, however. Minton (1956 and personal communication) cautioned against using venom data for determining definite relationships and suggested that they be used in conjunction with other data.
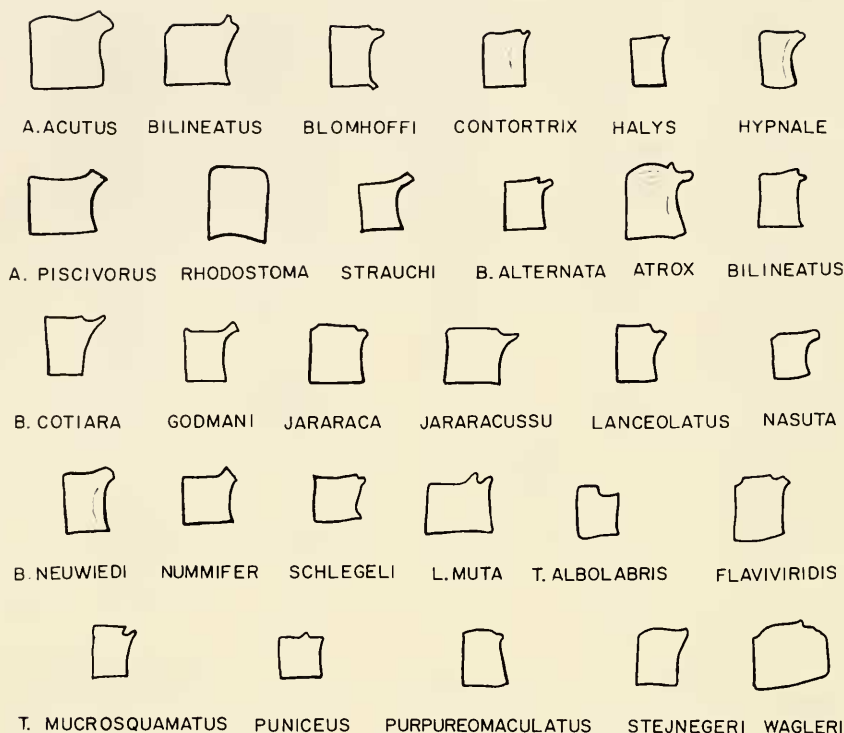
Fig. 20. Frontals of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*.

Mosauer (1932, 1935) studied the trunk muscles of several snakes, including *Crotalus horridus*, *Agkistrodon mokasen*, *A. piscivorus*, *Lachesis muta*, and *Sistrurus catenatus*. He found no major differences in trunk musculature among the crotalids examined. No one has studied the head muscles of crotalids as Haas (1952) did for viperids.

Scale characters in reptiles are one of the most important criteria used by modern herpetologists to determine relationships. In addition, Picado (1931) showed the usefulness of epidermal micro-ornaments in determining relationships in snakes, but no one has carried his investigations to other species and genera. On the basis of scale characters, relationships of crotalids were suggested by Amaral (1929), Klauber (1936a, 1952, 1956), Gloyd (1940), Gloyd and Conant (1943), and H. M. Smith (1946).

Though vibration of the tail occurs in many snakes, the rattle is unique in *Sistrurus* and *Crotalus*. A structure resembling an incipient rattle is found in the caudal spine and four rows of subcaudal scales in *Lachesis muta*. The rattle was discussed in great detail by Klauber (1940) and by Zimmermann and Pope (1948) and was used by Klauber (1956) in determining relationships. Probably the rattle was evolved only once (in a proto-*Crotalus-Sistrurus*), primarily as a defense against being stepped upon by large hoofed mammals, as suggested by Klauber (1940, 1956).

Color and color pattern are occasionally useful in determining relationships between species. This is especially true with many rattlesnakes. For example, the evolution of color pattern in the *Sistrurus ravus-Crotalus triseriatus* complex was discussed in detail by Gloyd (1940:244). Klauber (1956) also took color and pattern into account in the construction of his phylogenetic chart.
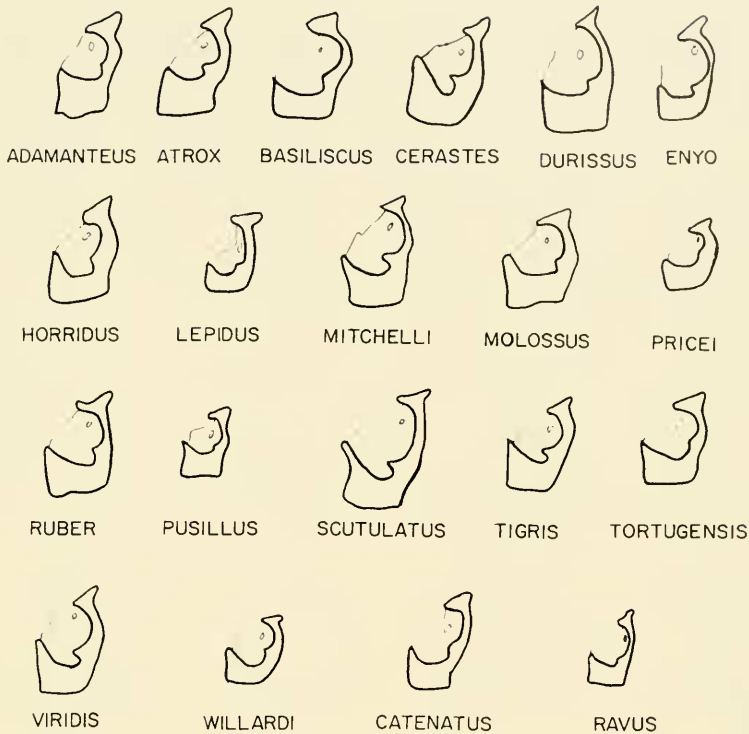
Fig. 21. Maxillae of species of *Crotalus* and *Sistrurus*.

The few interspecific crotalid hybrids (*Crotalus ruber* x *C. viridis helleri*, *C. durissus unicolor* x *C. scutulatus*, *C. horridus atricaudatus* x *C. adamanteus*, *C. viridis oreganus* x *C. scutulatus;* Klauber, 1956) do not add significantly to knowledge of relationships within the family. They indicate only that under rare circumstances in nature and in captivity isolating mechanisms may break down (or may never have developed, as in the case of *C. d. unicolor* and *C. scutulatus*) and hybridization will occur. One intergeneric hybrid (*C. h. horridus* x *S. c. catenatus*) reported by Bailey (1942) is of interest in further indicating the close relationship between *Crotalus* and *Sistrurus*.

METHODS

All phylogenies are somewhat subjective, as they indicate the worker's concept of relationship within a group. In this paper, the various characteristics of each species of crotalid are compared in order to determine relationships as accurately as possible. This comparison is made with drawings of bones (figs. 15 to 32) and a tabulation of characters (tables 10 to 12) for the species available. In order to determine the relationships among members of each genus, these tables are summarized in a series of additional tables (13 to 16), which give the number and percentage of characters that each species has in common with each other member of its genus. The following discussion of the phylogeny of the pit vipers is based primarily on the osteology and hence on the similarities and differences shown in tables 13 to 16. This basis is taken for two reasons: first, osteological characters are generally regarded as the most basic or least changeable and hence as more likely to indicate relationships than are features of the external morphology; and second, extensive data for other characters are not available except in *Crotalus* and *Sistrurus*. Data concerning venoms, hemipenes, scutellation, etc., have been used when available.
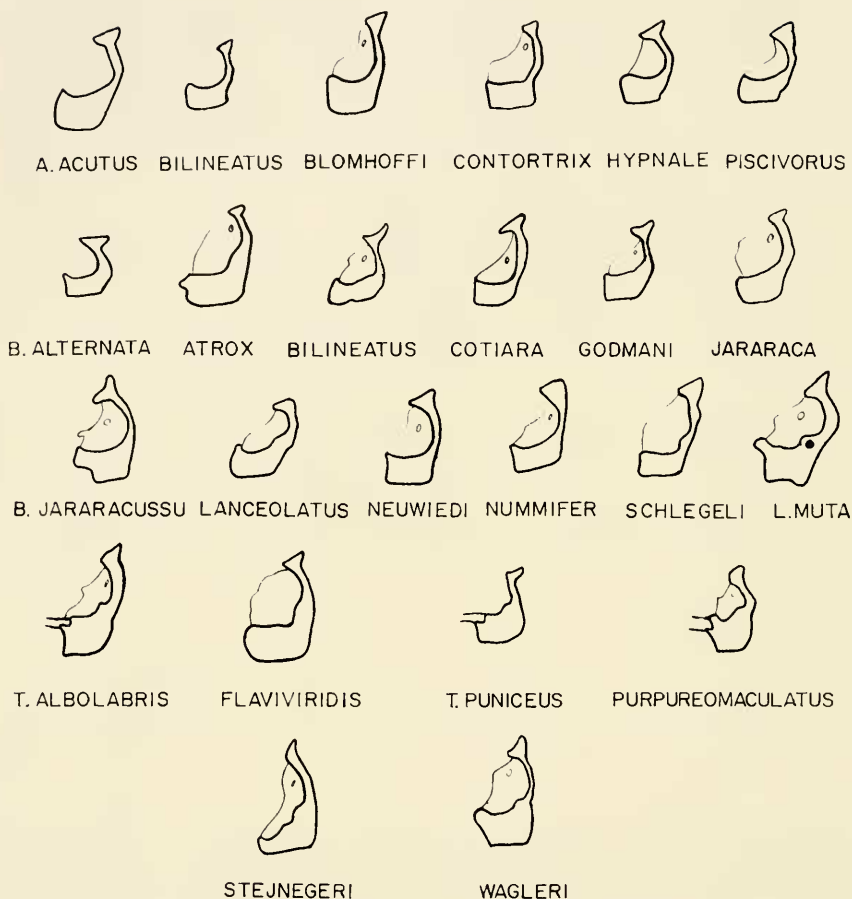
Fig. 22. Maxillae of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*.

At one time in the analysis of the phylogeny of crotalids, I considered weighting characters, giving more weight to those that are more stable intraspecifically. In approximate order of decreasing consistency and hence of decreasing usefulness in determining relationships, the various bones are: frontal, parietal, postfrontal, maxillary (especially the pit cavity), basisphenoid-basioccipital complex, prefrontals, squamosals, palatine, pterygoid, ectopterygoid, lower jaw, premaxilla, nasals, vertebrae, shaker, and ribs. But the weighting of characters is in itself subjective unless an analysis of variability is made for each character. I have therefore followed the procedure outlined above, comparing percentages of unweighted characters.

The terms "group" and "subgroup" denote only groups of related species, and the terms are not to be taken as equal in the different genera.

Most of the characters listed in tables 10 to 12 are sufficiently consistent to be useful in a key to skulls. Several keys to crotalids and crotalid skulls were made at the request of L. M. Klauber for his book (Klauber, 1956). These keys are used most successfully on adult skulls and in conjunction with the figures and tables presented here.

Fig. 23. Parietals and postfrontals of species of *Crotalus* and *Sistrurus*.

INTERGENERIC RELATIONSHIPS

The Solenoglypha, comprising the Crotalidae and the Viperidae, is characterized by the presence of movable fangs. Various osteological and myological studies (Haas, 1952; Johnson, 1955b, 1956) indicate that the Viperidae is more primitive than the Crotalidae. The Crotalidae also seems to be more specialized than the Viperidae in having the heat-sensitive loreal pit. The problems of the origin of the Solenoglypha (Boulenger, 1896; Hewitt, 1911; Mehely, 1911; Radovanovic, 1935; Haas, 1938, 1952) and of the differentiation of the two families, however, are not within the scope of this paper.

The most primitive genus of crotalids supposedly would have more characters in common with the more primitive Viperidae than would other crotalids. This genus would be the least divergent from its ancestor. *Trimeresurus* and *Agkistrodon* have more viperid characters than do *Bothrops, Lachesis, Sistrurus* and *Crotalus*. The pterygoid teeth extend beyond the junction of the ectopterygoid in *Agkistrodon, Bothrops,* and *Trimeresurus,* as they do in the Viperidae. The palatine in *T. wagleri* and in some species of *Agkistrodon* is short and stubby and similar to that in the Viperidae. The anterior end of the ectopterygoid is viperid-like in most species of *Trimeresurus*. The species of *Trimeresurus* also have relatively small loreal pit cavities — seemingly a primitive character. The members of the genus *Agkistrodon* all have large head plates, as do the primitive members of the Viperidae. *Sistrurus* also has large head plates, but most of its osteological characters and the presence of a rattle indicate that it is a more specialized genus. Minton (1956) noted that the venom of *Agkistrodon* is that of a relatively primitive crotalid stock. These characters all suggest that *Agkistrodon* and *Trimeresurus* are the most primitive genera in the Crotalidae. To judge from these and from other characters discussed below, *T. wagleri* and the small species of *Agkistrodon* (*contortrix, halys, hypnale, blomhoffi,* etc.) are probably the most primitive members of their genera and hence the most primitive members of the family.

Figure 33 is my concept of the relationships of the genera within the Crotalidae. This chart is based primarily on osteology. Superimposed on this phylogenetic tree are two major external characters: type of head scales and presence or absence of a rattle. There are large head plates in *Agkistrodon* and *Sistrurus* and small scales on the top of the head in *Bothrops, Trimeresurus, Lachesis,* and *Crotalus*. The head scales are keeled in *Bothrops, Lachesis,* and *T. wagleri*. The head scales anterior to the parietal region are not keeled in the remaining species of *Trimeresurus*.

Lachesis. — The relationship of the bushmaster, *Lachesis muta,* has been uncertain. It has been included in the same genus (*Lachesis*) with all of the species currently in *Bothrops* (Brazil, 1914). The species of *Trimeresurus, Lachesis,* and *Bothrops* have all been included in the same genus, or the species have been variously separated into the three genera. Most modern herpetologists have considered *Lachesis* a distinct genus but have still thought its relationships to be with *Bothrops*. As Garman (1889) first pointed out and as Ruiz (1951) also hinted, however, *Lachesis muta* is much closer to the rattlesnakes than to *Bothrops*. This similarity is especially evident in the osteology, wherein the majority of the characteristics of *Lachesis* are *Crotalus*-like. Notably, the pterygoid teeth do not extend beyond the middle of the junction of the ectopterygoid in *Lachesis, Crotalus,* and *Sistrurus,* and these forms are similar in having a knob-like process in the curvature of the pit-cavity. Other similarities are in the shapes of the prefrontals, parietal, squamosals, basioccipital, palatines, pterygoids, and ectopterygoids (tables 10, 11). The subcaudal scutes of *Lachesis* are in four rows posteriorly, in contrast to the one or two rows in all other crotalids. These scutes and the horny terminal spine probably resemble those of the *Sistrurus-Crotalus* ancestor before the rattle was perfected. The only major similarity of *Lachesis* and *Bothrops* is in their large size, but the subtropical *Crotalus durissus* is also large. The large size of these forms is in accordance with Bergmann's rule for ectotherms in the tropics, as discussed by Cowles (1945). The large size of the scales
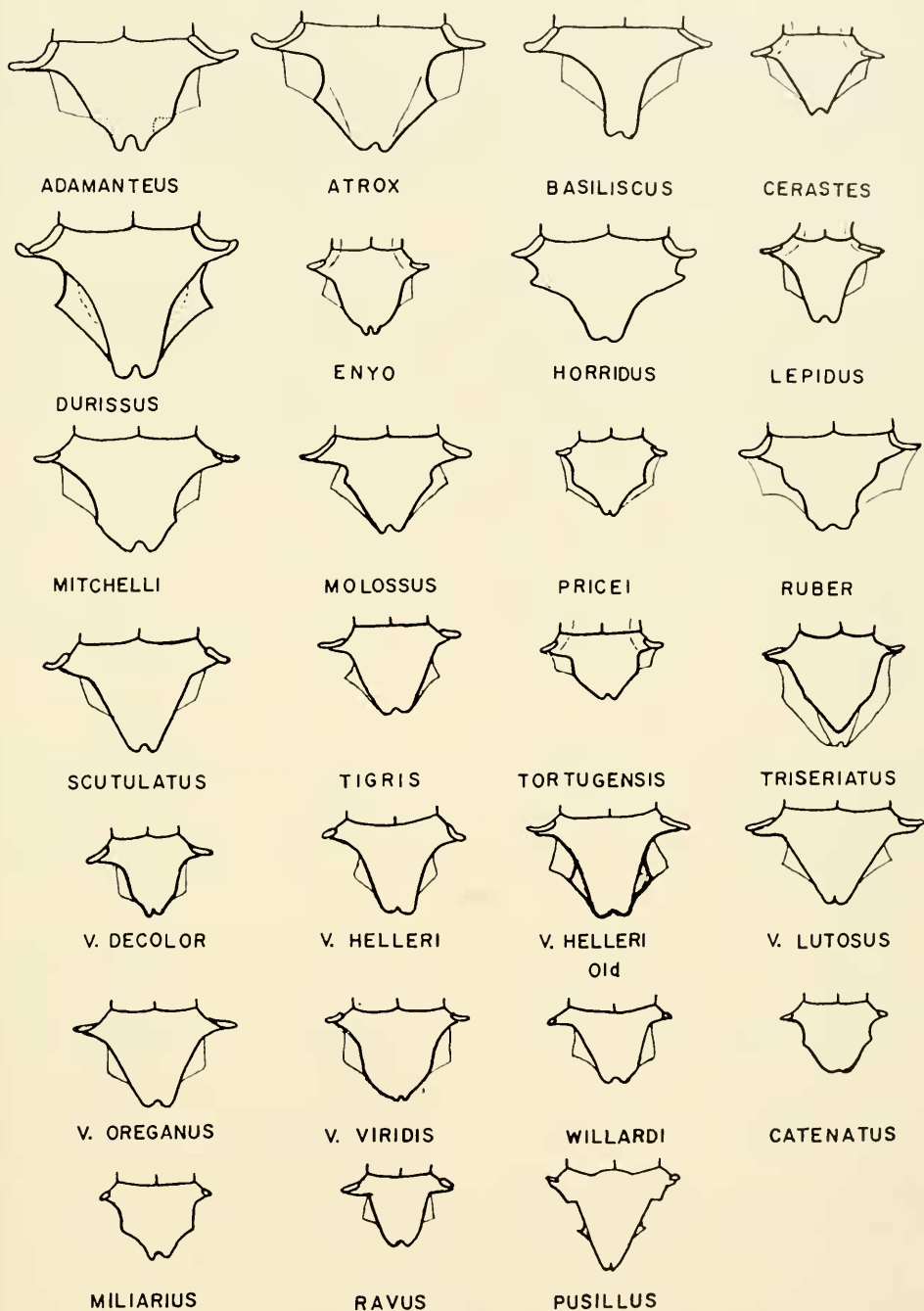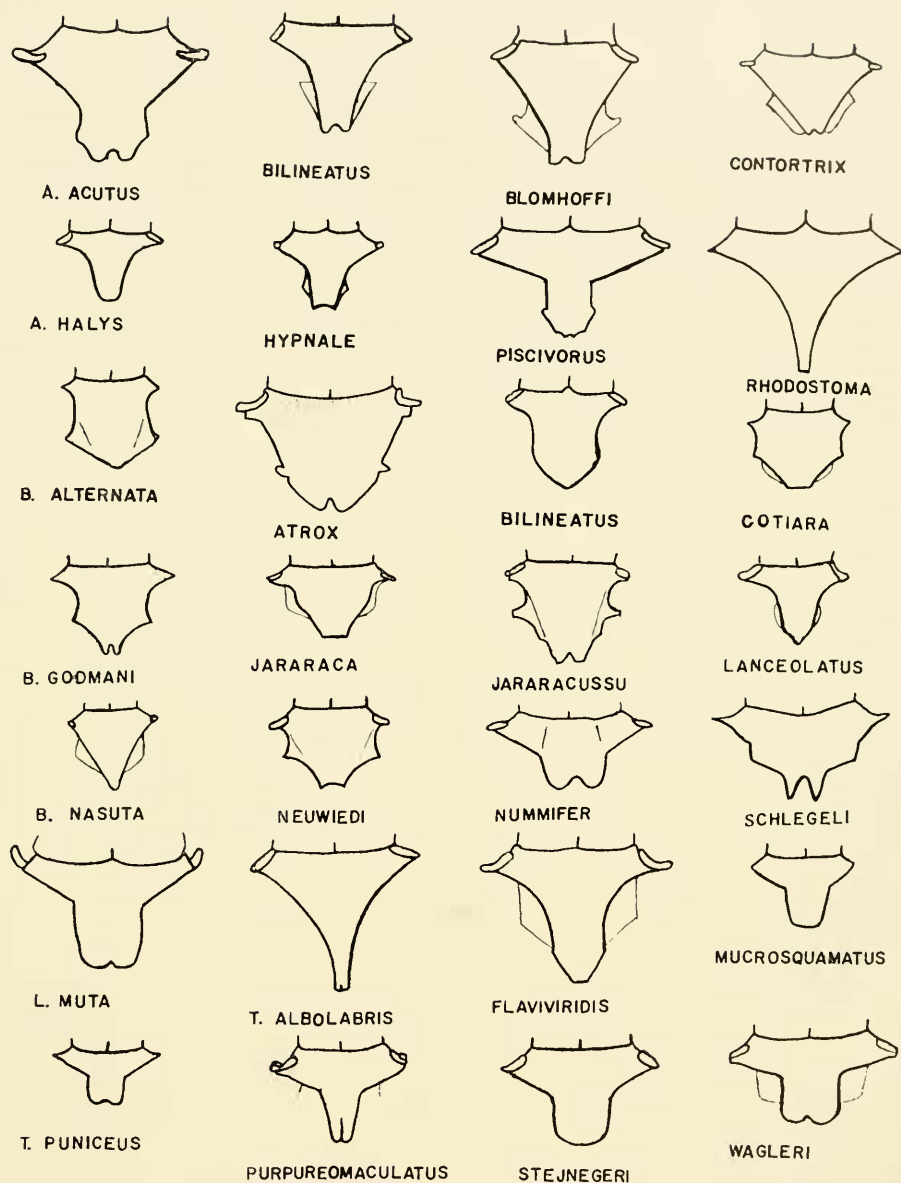
Fig. 24. Parietals and postfrontals of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*.

on the body of *Lachesis*, *C. durissus*, and the large species of *Bothrops*, may well be an example of convergence; it may be an adaptation of scale size in tropical regions for a primitive insulating mechanism for trapping and retaining non-movable air close to the body, as suggested by observations by Cowles (1958 and MS).

TABLE 10
Comparative osteology of *Agkistrodon* and *Lachesis*.

Species	Premaxilla		Nasal		Frontal			Postfrontal		Prefrontal		Processes	
	dorsal process	anterior edge	shape	process present	shape	ant. lat. process	Parietal shape	touches frontal	shape	shape	longest	fused	shortest
A. acutus	tri.	pointed	tri.	—	sq.	simple	broad T	no	curved	elong.	2 & 3	2 & 3	1
A. bilineatus	tri.	round	tri.	+	sq.	slight fork	broad T	yes*	short	short & stubby	2 & 3	0	1
A. piscivorus	tri.	round	tri.	—	sq.[1]	simple	broad T*	no	elong.	short	equal	0	1 or 2 or equal
A. blomhoffi	thin tri.	pointed	tri.	—	elong.	simple	tri.	yes	elong.	short & stubby	3	2 & 3	1
A. contortrix	tri.	pointed	elong. tri.	—	elong.*	simple	tri.	no	short	short & stubby	—— Variable ——		
A. halys	tri.	flat	elong. trap.	—	elong.	slight fork	tri.	yes	short				
A. hypnale	tri.	round	elong. rect.	—	elong.	simple	elong. T	no	short	short	3	2 & 3	1
A. rhodostoma	thin	round	tri.	—	elong.	simple	elong. tri.			elong.			
A. strauchi				—	elong.	simple but elong.	tri.-trap.	yes	short				
L. muta	tri.	flat	rect.	—	wider than long	forked	broad T	no	elong.		2 & 3*	2 & 3*	1

Symbols and abbreviations: +, present; ——, absent; 0, none; *, typical or average (deviations are usually discussed in the text section on osteology); ant., anterior; dep. ant., depression extending anteriorly; d. or dor., dorsal; ecto., ectopterygoid; el. or elong., elongate; lat., lateral; L., long; long., longest; Meck., Meckelian (in reference to the posterior Meckelian foramen); mid., middle; pal., palatine; post., posterior; proc., process; ptg., pterygoid; rect., rectangular; sq., square; str., straight; trap., trapezoidal; tri., triangular; v. or vent., ventral.

[1] To wider than long.
[2] Ectopterygoid longer than basal portion of pterygoid.
[3] A process present followed by a depression and another depression present on the outer face of the process.

TABLE 10 (Continued)

	Squamosal		Quadrate shape	Palatine shape	Ectopterygoid		Pterygoid medial curve	Maxilla cavity shape	Basisphenoid process		Longest Dent. proc.	Meck. foramen	
	shape	process			longer b. ptg.²	ant. lat. process			shape	hump		shape	process below
A. acutus	rect.	—	rect.	tall, fork	yes	brd. & flt.	mid. 1/3	simple	tri.	+	equal	elong.	—
A. bilineatus	rect.	—	rect.	tall, hump	no	broad	mid. 1/3	simple	rect.	+	vent.	elong.	—
A. piscivorus	rect.	+	broad rect.	tall, hump	no	broad	mid. 1/3	simple	rect.*	+*	dorsal	elong.	—
A. blomhoffi	curved	—	rect.	tall, hump	no	elong.	post. 1/2	simple	low	+	vent.	elong.	—
A. contortrix	rect.	—	rect.	low	no	broad	mid. 1/3	simple	low, tri.	+	vent.	elong.	—
A. halys	curved	—	rect.	low, hump	no	elong.		simple?	low	+	vent.	elong.	—
A. hypnale	rect.	—	rect.	low	no	broad	mid. 1/3	simple	low	+	dorsal	elong.	—
A. rhodostoma	rect.	—	rect.				post. 1/3	simple			vent.	elong.	—
A. strauchi	rect.	+	rect.	low, hump	yes			simple?	low		dorsal	elong.	—
L. muta	rect.	knob	rect.	tri, hump		broad	post. 1/2	proc. plus depr.?³	tri.-rect.	—	vent.	small	—
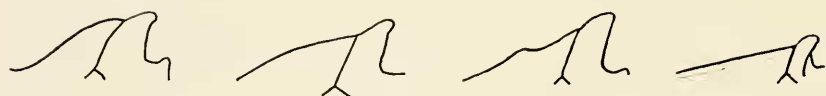
| ADAMANTEUS | ATROX | BASILISCUS | CERASTES |

| DURISSUS | ENYO | HORRIDUS | LEPIDUS |

| MITCHELLI | MOLOSSUS | PRICEI | RUBER |

| SCUTULATUS | TIGRIS | TORTUGENSIS | TRISERIATUS |

| VIRIDIS DECOLOR | VIRIDIS HELLERI | VIRIDIS OREGANUS WASH.–IDA. |

| VIRIDIS OREGANUS SIERRA | VIRIDIS VIRIDIS | WILLARDI |

| CATENATUS | MILIARIUS | RAVUS | PUSILLUS |
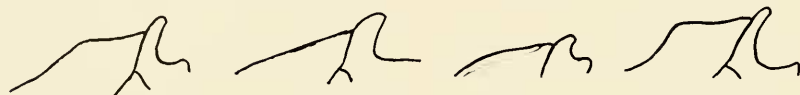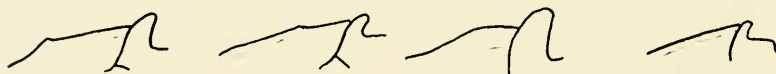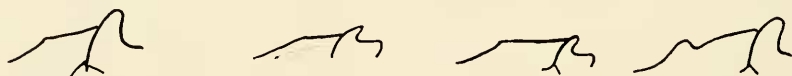
Fig. 25. Basioccipitals and basisphenoids of species of *Crotalus* and *Sistrurus*. The bones are drawn upside down and as viewed from the side.

Crotalus and *Sistrurus*. — As has just been stated, *Crotalus*, *Sistrurus*, and *Lachesis* are probably closely related, to judge by their osteology and caudal scutellation. *Agkistrodon* seems a more likely ancestor of a *Crotalus-Sistrurus-Lachesis* stock than does either *Bothrops* or *Trimeresurus*. In *Agkistrodon*, *Lachesis*, *Crotalus*, and *Sistrurus*, the greatest breadth of the head is due to the width of the parietal plus the poison glands. In *Trimeresurus* and *Bothrops*,
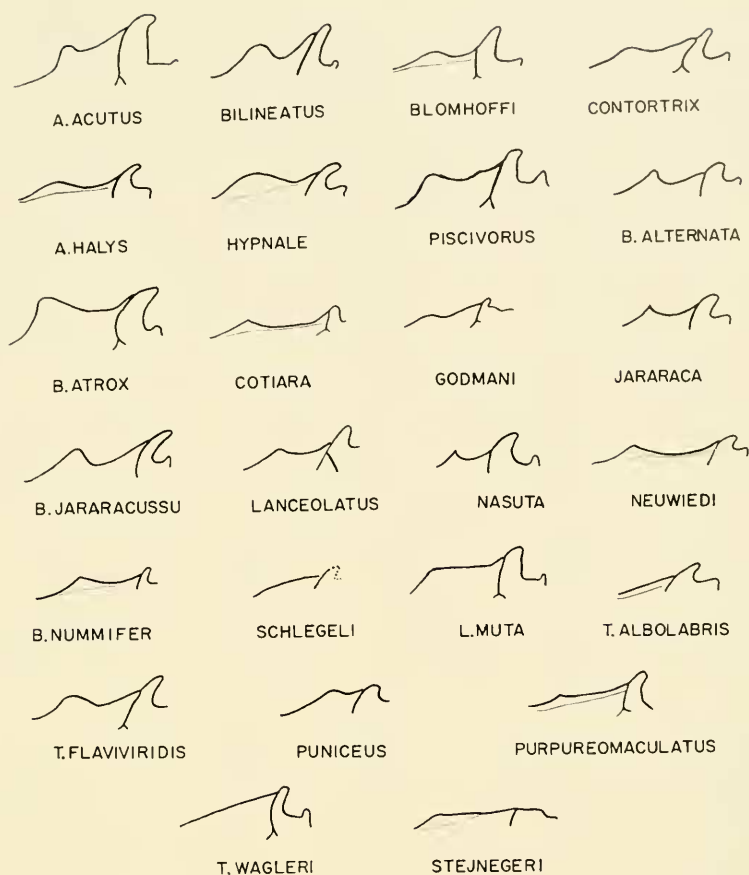
Fig. 26. Basioccipitals and basisphenoids of species of *Agkistrodon, Bothrops, Lachesis,* and *Trimeresurus*. The bones are drawn upside down and as viewed from the side.

however, the greatest breadth of the head is due to the extremely elongate quadrate and squamosal. This gives a pronounced triangular shape to the head. *Agkistrodon* has large head plates, as does *Sistrurus*. If *Sistrurus* and the *triseriatus* group of rattlesnakes are considered the most primitive members of the *Crotalus-Sistrurus* stock (see below), then one of the small species of *Agkistrodon* (*contortrix, hypnale, halys, blomhoffi*) seems the most likely ancestor of this stock. This is suggested by the shape of the frontal, parietal, and basisphenoid (tables 10 to 12). The *durissus* group might instead be considered the most primitive member of the *Crotalus-Sistrurus* stock; then the *Agkistrodon acutus-bilineatus-piscivorus* stock would be the most likely ancestor of the *Crotalus-Sistrurus-Lachesis* line. The latter relationship is suggested by similarity in the shape of the parietal, the prefrontal processes, the frontal, and the basisphenoid process (tables 10 to 12) in *Lachesis, Crotalus durissus,* and the *Agkistrodon acutus-bilineatus-piscivorus* group. The first relationship seems more likely, though neither can be proven as yet. It is apparent from the above and from figure 33 that, regardless of the relationships, small head scales have evolved several times in crotalids — in a proto-*Bothrops-Trimeresurus,* in *Lachesis,* and in *Crotalus.*

Fig. 27. Squamosals of species of *Crotalus* and *Sistrurus*.

Bothrops and *Trimeresurus*. — A major problem in the taxonomy of the Crotalidae is the question of the distinctness of the genera *Bothrops* and *Trimeresurus*. Both genera are tropical, the former in the New World, the latter in the Old, and many species in the two genera have similar colorations. No extensive work has been done on the taxonomy of the two genera except that of Maslin (1942) and Burger (MS). The two genera are quite distinct osteologi-cally, though this distinctness is based on a combination of several characters. There are two relatively exclusive characters. First, the curvature of the pit cavity bears a small process in *Trimeresurus*, whereas it is smooth in *Bothrops*, except in *B. schlegeli*, in which a process is slightly developed. Second, the palatine is entire in *Trimeresurus* and forked in *Bothrops*, except in *B. schlegeli* and *B. nummifer*. The major problem in distinguishing the two genera lies in certain similarities of these two species of *Bothrops* and *Trimeresurus wagleri* in the
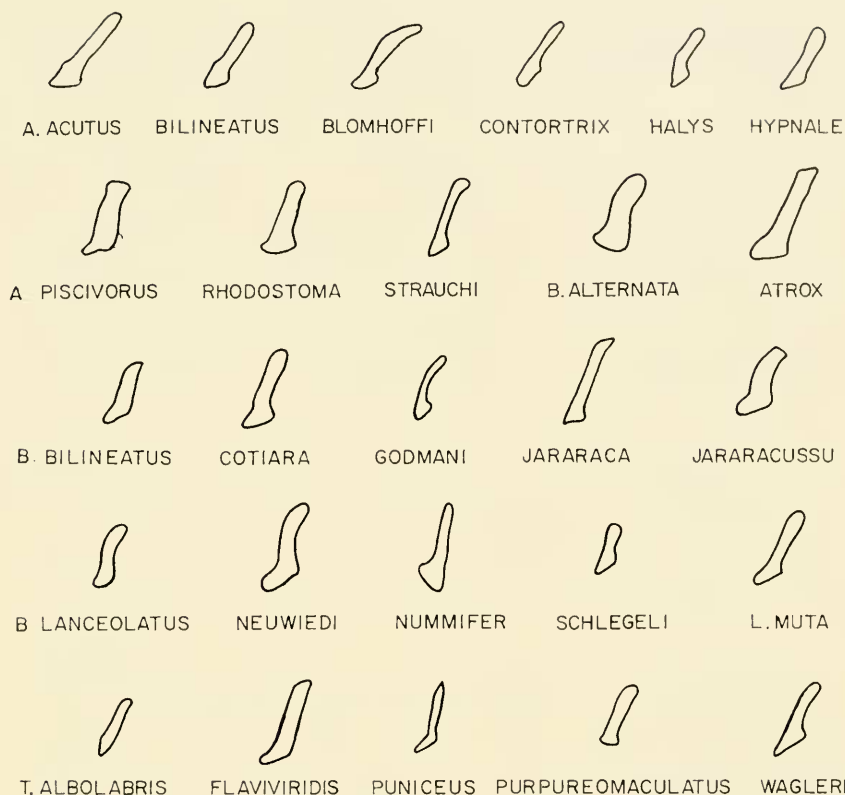
Fig. 28. Squamosals of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*.

shapes of the prefrontal, frontal, parietal, and postfrontal, and, according to Maslin (1942), in hemipenes and in scutellation. *Trimeresurus wagleri* is distinct from most species of *Trimeresurus* in its wide and depressed frontals, in its scutellation (Maslin, 1942), and in its neurotoxic venom (M.A. Smith, 1931; Maslin, 1942). It differs from *B. schlegeli* and *B. nummifer* in its elongate prefrontal, its low palatine, and its triangular basisphenoid. It differs from all other species of *Bothrops* in having a process in the curvature of the pit cavity. Perhaps most importantly, it differs from all other crotalids in having the lower lumen of the fang medial rather than anterior and in having depressed frontals. *Trimeresurus wagleri* thus can be distinguished from the small species of *Bothrops* as well as from the other species of *Bothrops* and *Trimeresurus*. The other species of the two genera are easily separable on the basis of the two major characters mentioned above. As will be discussed below, the distinctness of *T. wagleri* and of the small *Bothrops* will be recognized by placing them in separate subgenera within their respective genera.

PHYLOGENY OF *AGKISTRODON*

Little has been said in the literature concerning the relationships of the species of *Agkistrodon*. Nevertheless, many workers have been concerned over the occurrence of the same genus in North America and in Asia. Some have supposed that the two groups were not in the same genus, although no evidence supporting this supposition has been presented. The present study shows that there are no major osteological characters to distinguish all Old World from all New World species of *Agkistrodon*. Most of the characters shared by Old
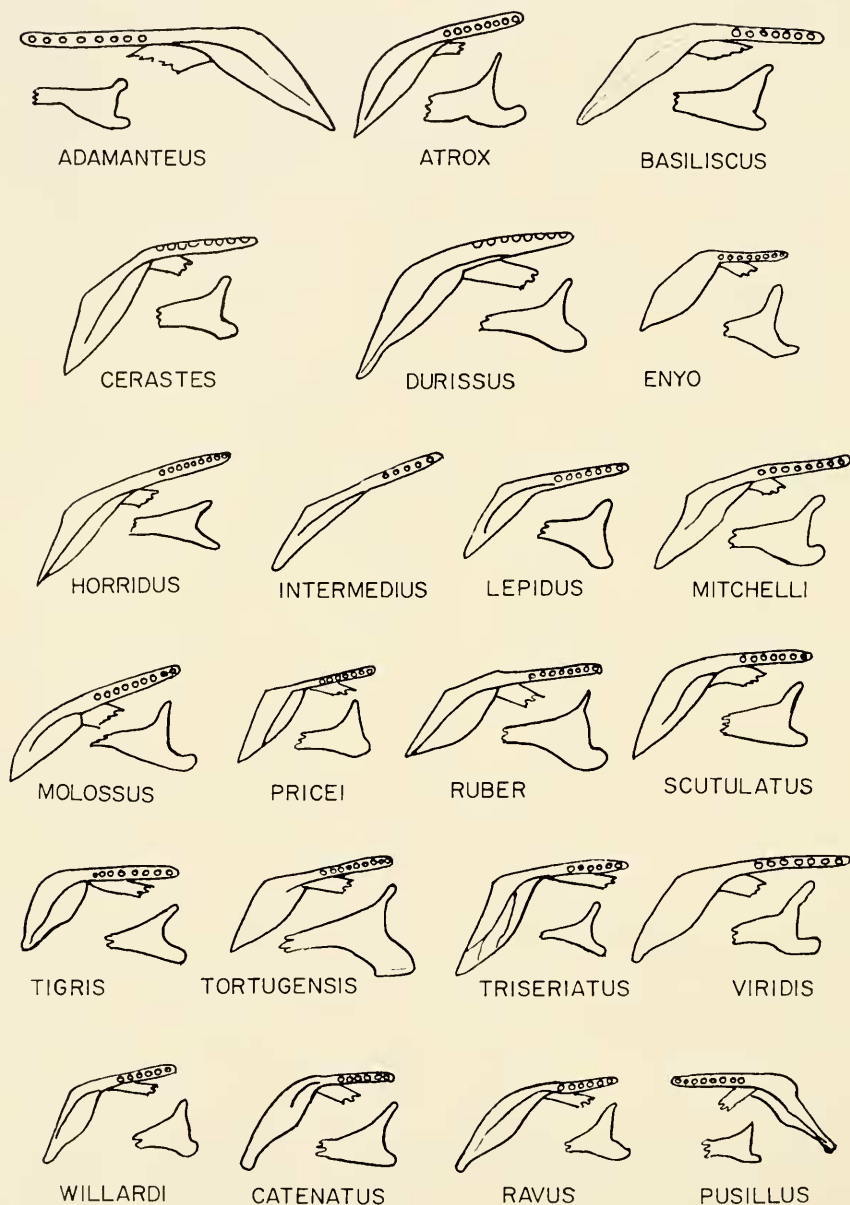
Fig. 29. Pterygoids and ectopterygoids of species of *Crotalus* and *Sistrurus*.

The pterygoids are shown in ventral view, the ectopterygoids in dorsal view (anterior ends). The junction of the two bones is indicated in the drawing of the pterygoid. Teeth are indicated by circles, the mean number for each species being shown.

World forms or by New World forms are also shared by other members of the genus. *Agkistrodon contortrix* and the *piscivorus-bilineatus* group show closer osteological relationships to various Asiatic forms than they do to each other (table 13).
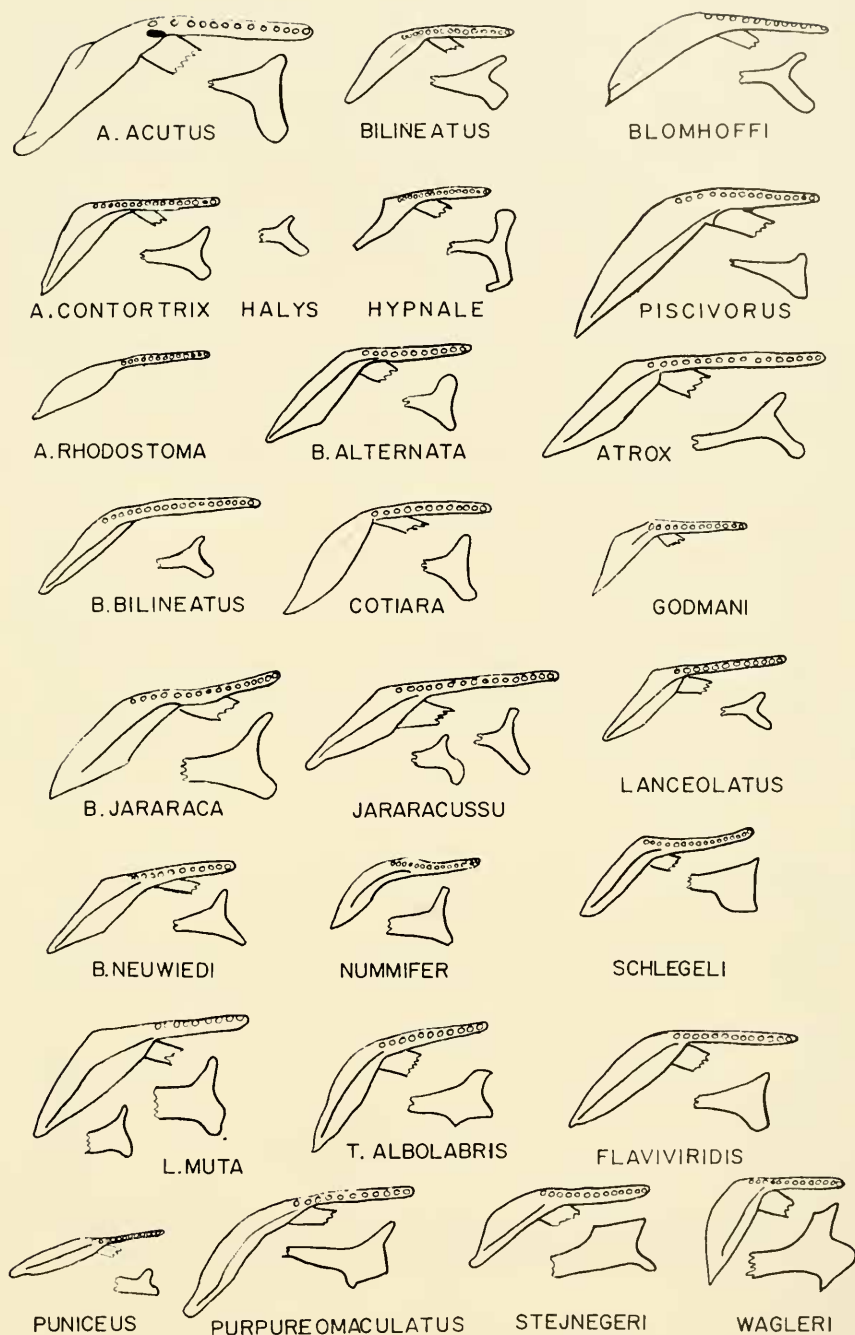
Fig. 30. Pterygoids and ectopterygoids of species of *Agkistrodon, Bothrops, Lachesis,* and *Trimeresurus.* See caption of figure 29.

TABLE 11

Comparative osteology of *Crotalus* and *Sistrurus*. Symbols and abbreviations as in table 10.

Species	Premaxilla dorsal process	Premaxilla ant. edge	Nasal shape	Nasal process present	Frontal shape	Frontal ant. lat. process	Parietal shape	Postfrontal touches frontal	Postfrontal shape	Prefrontal shape	Processes longest	Processes fused	Processes short	Palatine shape
C. *durissus*	thick	flat	rect.*	+	sq.	forked	elong. tri.	+	elong.	rect.	2 & 3	2 & 3	1	tri.
basiliscus	thick	flat	rect.*	—	sq.*	forked	elong. tri.	+	rect.	elong.	2 & 3	2 & 3	1	tri.
horridus	thin	flat*	rect.*	—*	sq.*	forked	broad tri.	—*	rect.	rect.	2	0	·3	tri.
molossus	thick	flat	sq.	+*	sq.	forked	broad tri.	+*	elong.	rect.	2 & 3	0	1	tri.
adamanteus	thin	flat-curv*	sq.*	+	sq.*	forked	broad tri.*	+	elong.	rect.	2 & 3	2 & 3	1	tri.
atrox	thin	flat-curv*	sq.	+	sq.*	forked	broad tri.*	+	elong.	rect.	2	2 & 3	1	tri.
tortugensis			rect.	—	elong.	forked	broad tri.	+*	elong.	rect.	2 & 3	0	1	tri.
ruber	thin	curv*	rect.*	+	sq.	forked	broad tri.	—	elong.	sq.	2	0*	1	tri.
scutulatus	thin	flat*	rect.	—	elong.	forked	elong. tri.	—	rect.	rect.	2 & 3	0	1	tri.
viridis	thin*	point.	sq.*	—*	elong.	forked	broad tri.	—*	rect.	rect.	2	0	1	tri.
mitchelli	thick	flat*	sq.	+	elong.	simple	broad tri.	—	rect.	rect.	2 & 3	2 & 3	1	tri.
tigris	thin	flat	rect.	—	elong.	forked	broad tri.	—	rect.	rect.	2	0	1	tri.
cerastes	thin	flat	sq.-rect.	—*	elong.	forked	broad tri.	—	small rect.	rect.	2	0	1	tri.
enyo	thin	flat*	sq.	—	elong.	forked	broad tri.	—	small rect.	rect.	2	0	3	tri.
lepidus	low	flat	rect.	—*	elong.	simple	elong. tri.	—	small rect.	rect.		0	1	tri.
pricei	thin	curv*	rect.	—	elong.	forked	broad tri.	—	small rect.	stubby	2	0	3	tri.
triseriatus	thick	flat	rect.	—	elong.	forked	broad tri.	—	elong.	rect.	2	0	3	low
willardi	thin	point. flat	sq.	—	elong.	forked	broad tri.	—	oval	rect.	2	0	1	low
pusillus	thick	flat	elong.	—	elong.	forked	elong. tri.	—	small oval	rect.	2	0	1	low
S. *catenatus*	thin	point.	rect.	—*	elong.	forked	broad trap.	—	small oval	rect.	2 & 3	2 & 3	1	tri.
miliarius	thick	round	rect.	—	elong.	forked	broad trap.	—	small oval	rect.	2 & 3	0	1	
ravus		point. flat	rect.	—	elong.	forked	elong. tri.	—	rect.	stubby	2 & 3	2 & 3	1	tri.

TABLE 11 (Continued)

	Squamosal		Quadrate	Pterygoid	Ant. Process Ectopterygoid			Maxilla cavity			Basisphenoid process		Longest	Meck. foramen	
	shape	lat. proc. angle	shape	medial curve	widest	flat area between	shape lat. proc.	process present	depression present	dep. ant.	shape	hump	Dent. Proc.	shape	process below
C. durissus	curv.	90°	rect.	middle	lat.	+	broad	+	—	—	tri.	+	vent.	small	—
basiliscus	curv.	acute	rect.	post. 1/2	lat.	+	medium	+	—	—	tri.	+	vent.	small	—
horridus	curv.	90°	rect.	post. 1/2	lat.	+	medium	+	—	—	tri.	+	vent.	elong.	—
molossus	curv.	90°	rect.	post. 1/2	lat.	+	medium	+	—	—	tri.	+	vent.	small	+
adamanteus	curv.*	acute	rect.	post. 1/2	equal	+	medium	+	—	—	tri.	—*	vent.	small	—
atrox	curv.	obtuse	rect.	post. 1/2	lat.	+	broad	+	—	—	tri.	—	vent.	small	+
tortugensis	str.	acute	rect.	middle	lat.	+	turned ventrally	+	—	—	rect.	—	vent.	small	—
ruber	curv.	obtuse	rect.	middle	lat.	+	turned ventrally	+	+	—	rect.	—	vent.	elong.	+
scutulatus	crv./str.	90°- obtuse	rect.	middle	lat.	+	round	+	+	+	low-tri.	—	vent.	elong.	—
viridis	str.*	obtuse	rect.	middle	equal	+*	round	+	+	+	low	—	vent.	elong.	*
mitchelli	curv.*	obtuse	rect.	mid. & post.	lat.	+	round	+	+	+	rect.*	—	vent.	elong.	+
tigris	curv.	obtuse	rect.	middle	equal	—	medium	+	+	+	low	—	vent.	elong.	—
cerastes	curv.	obtuse	rect.	mid. & post.	lat.	—	round	+	+	+	low	—	vent.	elong.	—
enyo	str.	obtuse	rect.	middle	median	+	pointed	+	+	+	low	—	vent.	elong.	—
lepidus	str./crv.	acute	rect.	middle	lat.	—	broad	low+	+	+	low	—	vent.	elong.	—
pricei	forked str.	reduced	rect.	middle	lat.	—	broad	+	—	—	low	—	vent.	elong.	
triseriatus	str.	90°	rect.	middle	lat.	+	medium + flap			—	low	—	vent.	elong.	—
willardi	str.	acute	rect.	middle	equal	+	medium	+			low	—	vent.	elong.	—
pusillus	str.	acute	rect.	middle	lat.	+	narrow	low+	—	—	tri.	+	vent.	elong.	—
S. catenatus	str.	acute	rect.	middle	lat.	+	medium	+	—	—	low	—	vent.	elong.	—
miliarius	str.	acute	rect.					+	—	—	low	—	vent.	elong.	—
ravus	str.	90°	rect.	middle	lat.	+	pointed	+	—	—	rect.	—	vent.	elong.	—
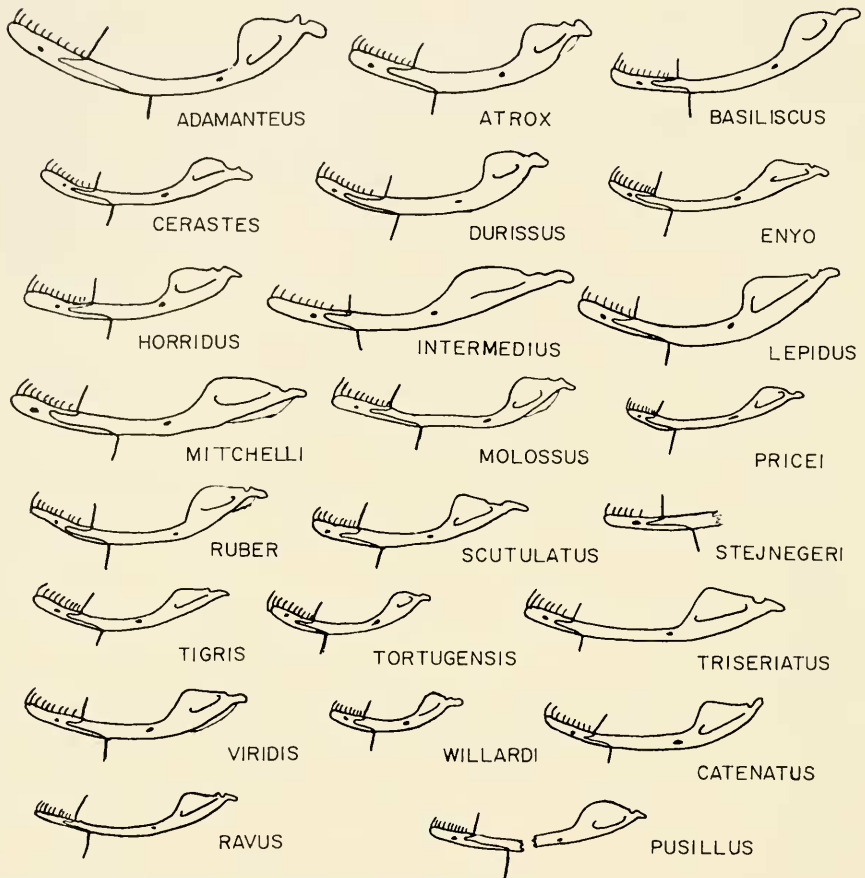
Fig. 31. Lower jaws of species of *Crotalus* and *Sistrurus*.
Teeth are indicated by simple lines, the mean number for the species being shown. The posterior extents of the dorsal and ventral posterior processes of the dentary are indicated by heavy lines.

Osteologically, the genus *Agkistrodon* is divisable into two main groups (fig. 34). One of these groups includes the Asian *acutus* and the North American *bilineatus* and *piscivorus*. The species in this group have 13 of 26 characters in common, including square frontals, T-shaped parietals, broader anterior ends to the ectopterygoids, and high basisphenoid processes (table 10). Within this group, *bilineatus* and *piscivorus* are closely related, being similar in most of the characters studied (tables 10, 13). *Agkistrodon bilineatus* is similar to *contortrix* in a few minor characters such as the ratio of the lower jaw length to quadrate length. According to Minton (1956), *bilineatus* is intermediate in several venom characters between *contortrix* and *piscivorus*. Gloyd and Conant (1943) suggested that *bilineatus* might be closely related to *mokeson* (= *contortrix*). From their Table I, it is apparent that *bilineatus* is similar to *mokeson* in scale rows and caudal scales. However, *bilineatus* is similar to *piscivorus* in the number of ventrals and infralabials. All osteological evidence indicates a close relationship of *bilineatus* and *piscivorus*. *Agkistrodon acutus* has several peculiar characteristics, such as a pointed premaxilla, an ectopterygoid process, and an elongate prefrontal. It still has, however, several characters that indicate relationship to *bilineatus* and *piscivorus*, such as a square frontal and a T-shaped parietal (table 10). *Agkistrodon acutus* is one of the few ovoviviparous crotalids (Pope, 1935).
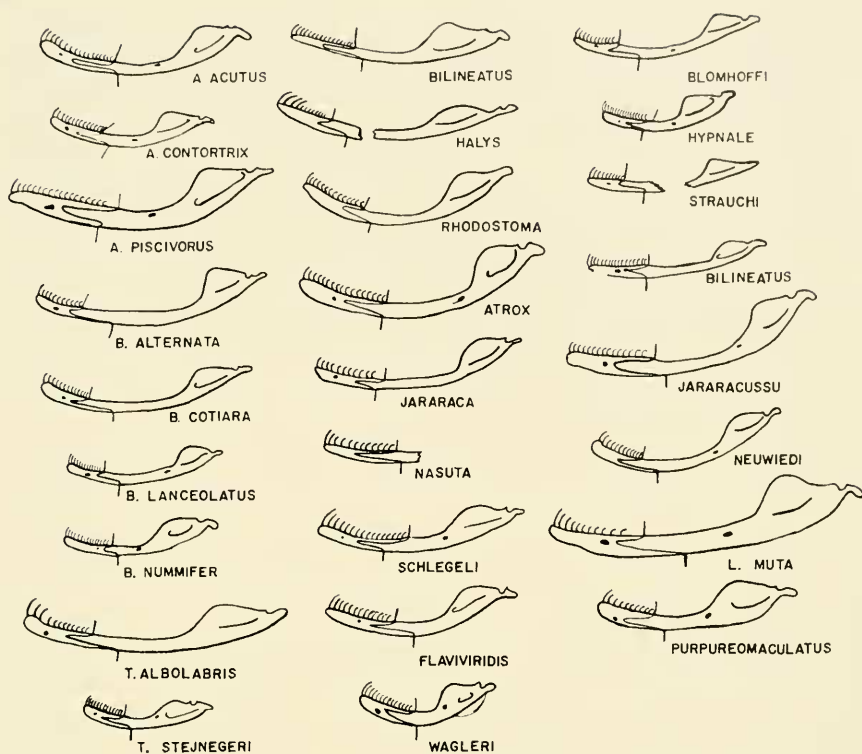
Fig. 32. Lower jaws of species of *Agkistrodon*, *Bothrops*, *Lachesis*, and *Trimeresurus*. See explanation under figure 31.

The second group of closely related species includes the New World *contortrix* and the remaining Asiatic species (*hypnale*, *halys*, *blomhoffi*, *rhodostoma*, etc.; fig. 34). The forms within this group have 8 of 14 characters in common (57.1 per cent). The most important of these characters are the elongate frontal, the triangular parietal, and the low basisphenoid. *Agkistrodon hypnale*, with its trapezoidal nasal and elongate parietal, seems the most divergent member of this group. *Agkistrodon blomhoffi* is similar in many respects to *halys*. The osteology of *rhodostoma* is known only from a drawing in M. A. Smith (1943: 498, fig. 158); *rhodostoma* appears to be quite specialized, but certain of its characteristics point to a relationship with the *hypnale* stock. It has a large number of characters in common with *hypnale* and *strauchi*. *Agkistrodon contortrix* is more closely related to the Old World forms such as *halys* and *hypnale* (fig. 34, tables 10, 13) than it is to either *bilineatus* or *piscivorus* of the New World. The relationship of *strauchi* to *hypnale*, of *nepa* to *hypnale*, and of *monticola* and *himalayanus* to *strauchi* (fig. 34) is suggested by comments on the external morphology of these forms by Pope (1935) and by M. A. Smith (1943). The relationship of *strauchi* to *hypnale* is also supported by osteological evidence. The phylogenetic positions of the rare *annamensis* and *millardi* are at present unknown. They may belong in the *hypnale-halys* subgroup (fig. 34).

Regardless of where the center of origin of the genus *Agkistrodon* was (though it was probably Asia), there are members of both major groups of the genus in the Old and New Worlds (fig. 34).

TABLE 12

Comparative osteology of *Bothrops* and *Trimeresurus*. Symbols and abbreviations as in table 10.

Species	Premaxilla		Nasal		Frontal		Parietal shape	Quadrate shape	Postfrontal		Prefrontal		Processes	
	dorsal process	ant. edge	shape	process present	shape	ant. lat. process			touches frontal	shape	shape	longest	fused	shortest
B. alternatus	thin	point.	el. rect.	—	elong.	forked	squarish	rect.	no	elong.	elong.	2 & 3	2 & 3	1
atrox	thick	point.	elong.	+	elong.	forked	squarish	rect.	no*	elong.	elong.	2 & 3	2 & 3	1
bilineatus	thin	round	el. tri.	—	square	forked	squarish	rect.	yes	elong.	elong.	2 & 3	2 & 3	1
godmani	thin	round	elong.	—	elong.	elong.	triangular	rect.	no	small	elong.	2 & 3	2 & 3	1
jararaca	thin	point.*	elong.	—	square	forked	triangular*	rect.	no	small	elong.	2 & 3	2 & 3	1
jararacussu	thick	point.	elong.	+	square	forked	triangular	rect.	no	elong.	elong.	2 & 3	2 & 3	1
lanceolatus	thick	point.	el. rect.	+	elong.	forked	triangular	rect.	yes	elong.	short, stubby	2 & 3	2 & 3	1
neuwiedi	thick	point.	el. rect.	—	elong.	simple	trap.	rect.	no*	rect.	elong.	2 & 3	2 & 3	1
cotiara	thick	point.	square	—	elong.	elong. & forked	squarish	rect.			elong.	2 & 3	2 & 3	1
nasuta					elong.	simple	triangular	rect.	no	small	rect.	2 & 3	2 & 3	1
nummifer	thin	round		—	wider than L.¹	simple	broad T	rect.	no	rect.	square	2 & 3	2 & 3	1
schlegeli	thin	round	elong.	—	wider than L.¹	forked	broad T	curved, rect.	no	rect.	square	2 & 3	0	1
T. gramineus	thick	flat	rect.	—	square	simple	triangular	el. tri.	yes	rect.	thin	1, 2, 3	0	0
flaviviridis	thick	round	rect.	+	elong.	forked	triangular	el. tri.	no	curved	elong.	1, 2, 3	0*	0
mucrosquamatus					elong.	forked	broad T	el. tri.			stubby	2 & 3	2 & 3	1
puniceus			rect.	—	square	simple				small oval	stubby			
purpureomaculatus	thick	round	rect.	—	elong.	simple	broad T*	rect.	no*	rect.	stubby	2	0	1
steinegeri					elong.	simple	broad T		no	rect.				
wagleri	thin	round	rect.	+	wider than L.¹	simple*	broad T	el. tri.	no	small oval	elong.	2 & 3*	2 & 3	1

¹Center of frontal depressed.

TABLE 12 (Continued)

|	Palatine shape	Squamosal shape	Squamosal lat. proc.	Ectop. ant. lat. proc.	Pterygoid medial curve	Maxilla cavity curvature	Basisphenoid process shape	Basisphenoid process hump	Longest dentary process	Meckelian foramen shape	Meckelian foramen process below	Position of lower lumen of fang
B. alternatus		stubby curved	—	thin, el.	middle	simple	tri.	+	ventral	elongate	—	anterior
atrox	forked	rect.	—	thin, el.	middle	simple	rect.	+	dorsal*	small*	—	anterior
bilineatus		rect.	—	medium	middle	simple	low	+	equal	elongate	—	anterior
godmani	forked	curved	+	broad	middle	simple	low	+	dorsal	elongate	—	anterior
jararaca	forked	rect.	—	broad	middle	simple	tri.	+	dorsal	small	—	anterior
jararacussu	forked	stubby curved	—	thin, el.*	post. ½	simple	tri.	+	ventral	small	—	anterior
lanceolatus	forked	curved	—	thin, el.	middle	simple + sm. knob	tri.	+	ventral	elongate	—	anterior
neuwiedi	forked	curved*	+	elong.	middle	simple	low	+	ventral	elongate	—	anterior
cotiara	forked	rect.	+	medium	middle	simple	low	+	ventral	elongate	—	anterior
nasuta							tri.	+	equal			anterior
nummifer	humped, no fork	rect.	+	broad	entire length	simple	low	+	ventral	small	—	anterior
schlegeli	humped, no fork	stubby	+	broad	middle	humped or knobbed	low	—	dorsal	elongate	—	anterior
T. gramineus	low	oval	—	broad	middle	humped	low	—	ventral	small	—	anterior
flaviviridis	hump	rect.	—	broad	middle	humped	tri.	+	ventral	elongate	—	anterior
mucrosquamatus				narrow		small hump	low			elongate	—	anterior
puniceus	hump	elong.	—	broad	none	small hump	tri.	+				anterior
purpureomaculatus	hump	rect.	+	broad	middle	humped	low	+	ventral	small	—	anterior
steinegeri				narrow	post. ½	small hump	low	—	ventral	elongate	—	anterior
wagleri	low	rect. curv.	+	flat & broad	middle	humped	tri.	—	ventral	small	+	medial
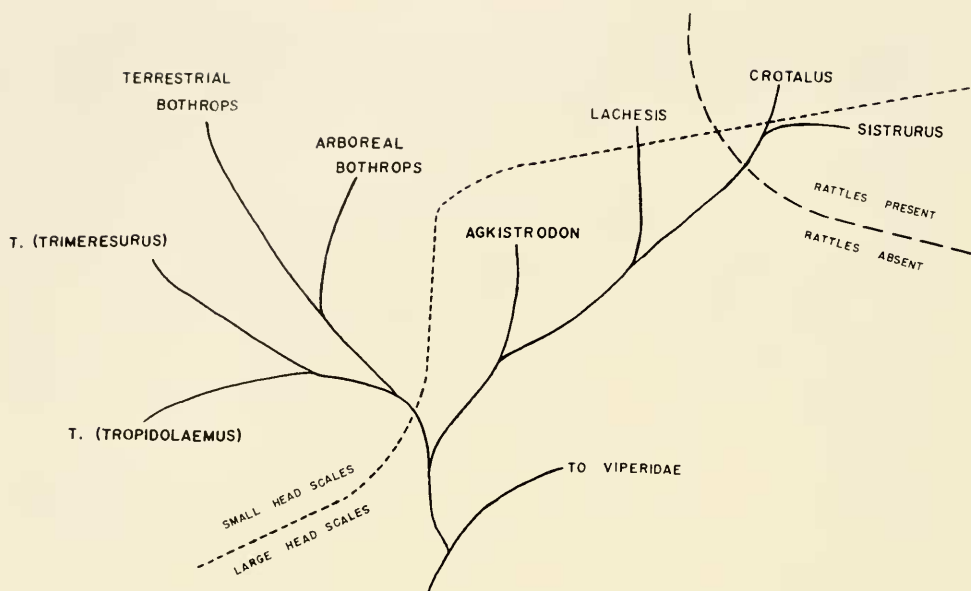
Fig. 33. Suggested phylogeny of the Crotalidae.

PHYLOGENY OF *CROTALUS* AND *SISTRURUS*

The genus *Crotalus*, as here defined (fig. 36), includes five main groups: *durissus*, *atrox*, *viridis*, *triseriatus*, and *Sistrurus*. These groups and the species within them have been recognized on the basis of external morphology (Gloyd, 1940; Klauber, 1956; H. M. Smith, 1946; Amaral, 1929). The relationships of the forms in the *triseriatus* group have been the least known. One of the groups, *Sistrurus*, is usually considered a separate genus. The *Sistrurus* group is similar in many of its characters (Amaral, 1929; Gloyd, 1940) to the *triseriatus* group. In my opinion, the characters that distinguish *Crotalus* and *Sistrurus* break down within *S. ravus*, *C. pusillus*, and *C. intermedius*. In general, the differences between *Crotalus* and *Sistrurus* are of the same type and order of magnitude as those between any of the groups of *Crotalus* (table 14).

The nine large plates on the top of the head, supposedly characteristic of *Sistrurus*, are broken up into smaller scales in a fair number of the specimens of *S. ravus* (Gloyd, 1940: 241-242). Klauber (1956:175) noted that the parietal scale often splits transversely in *S. ravus*. Fragmentation of the head plates also occurs as a rarity in *S. catenatus* and *S. miliarius streckeri* (Gloyd, *op. cit.*). This fragmentation of the head plates in some species of *Sistrurus* resembles the head scutellation of certain species of *Crotalus* (*intermedius*, *polystictus*, *pricei*, *pusillus*). The occurrence of fragmented head plates in rare individuals of *Sistrurus* does not invalidate the character of 9 head scales as diagnostic of *Sistrurus*, but it suggests that this character may not have as complex a genetic basis as thought by some.

In the hemipenes of *Sistrurus* there is a gradual transition from spines to calyces, whereas in those of *Crotalus* there is an abrupt change from spines to fringes (Gloyd, 1940). Unfortunately, descriptions are not available of the hemipenes of the crucial species, *S. ravus* and *C. pusillus*. Klauber (1956) pointed out that in *C. stejnegeri* and *C. lepidus* the transition from spines to calyces is not so sharp as in most species of *Crotalus*, and in fact is similar to that found in *Sistrurus*. He considered this condition unique with *stejnegeri* and *lepidus* rather than primitive or intermediate.
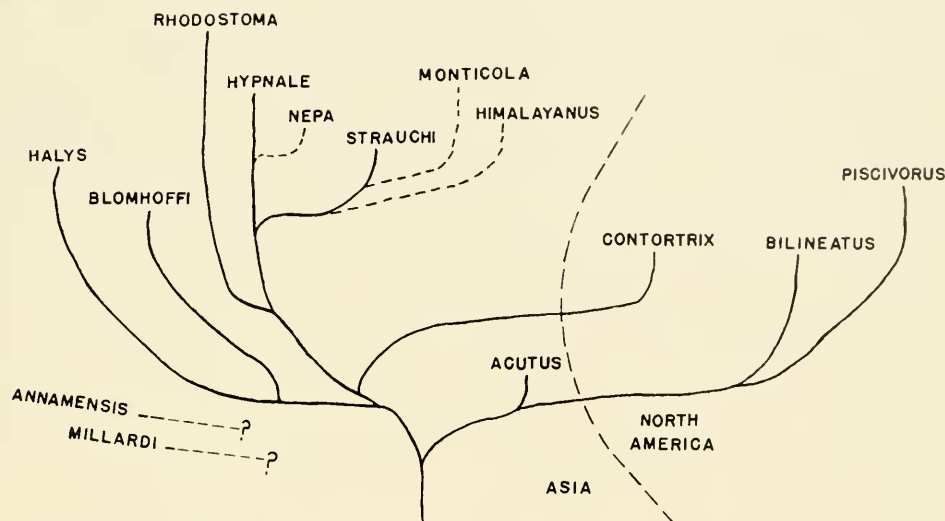
Fig. 34. Suggested phylogeny of *Agkistrodon*.

On the basis of its osteology, *Sistrurus* is similar to the *triseriatus* group of *Crotalus*, with 12 of 29 characters (41.4 per cent) in common. One of the supposed diagnostic features of *Sistrurus* is the acute angle formed by the posterolateral process of the squamosal. This angle is 80° or less in *S. catenatus* and *miliarius*. This is not a distinguishing character, however, for the angle is not acute in *S. ravus*, whereas it is acute in some of the small species of *Crotalus*, such as *pusillus* (table 11). Though the species of *Sistrurus* have many characters (72.7 per cent) in common, the group shares no character that distinguishes it from *Crotalus*. The distinctness of the two genera breaks down in the similarity of *S. ravus* to several members of the *triseriatus* group, especially *C. pusillus*. I therefore consider *Sistrurus* as a subgenus of *Crotalus*.

Sistrurus ravus is usually considered the most primitive member of the *Sistrurus* group (Gloyd, 1940; Klauber, 1956). This position is supported by osteological evidence, such as the shapes of the palatine, frontal, parietal, and prefrontal and the presence of a basisphenoid process. *Sistrurus ravus* is similar to *C. pusillus* in scutellation and osteology. *Sistrurus ravus* is the most *Crotalus*-like species in its group.

The osteology of *S. catenatus* and *miliarius* is very similar (87 per cent of characters in common, table 14). Minton (1956) noted that *miliarius* venom seems more primitive than *catenatus* venom. It is most probable that *catenatus* and *miliarius* represent separate branches from a primitive *ravus*-like form (fig. 36).

Two rattlesnakes, *C. polystictus* and *stejnegeri*, are unusual in head length, tail length, teeth, rattles, etc. (Klauber, 1952, 1956). The osteology of the rare *stejnegeri* (only 5 specimens known) is known only from counts of tooth sockets (table 6) and from a dentary bone. The latter has the dorsal process shorter than the ventral process. There are no palatine teeth. The osteology of the equally rare *polystictus* is unknown except that one specimen has 8 dentary, 7 pterygoid, and no palatine teeth. The dentary and pterygoid teeth are extremely thin and elongate but are wide at the base. The reduction of the palatine teeth and the unusual proportional and scutellation differences of these two species (Klauber, 1937, 1938, 1939, 1952, 1956) suggest that probably they are closely related and diverged from the main stock of rattlesnakes soon after one of the more primitive groups, *Sistrurus*.

TABLE 13

Numerical summary of relationships[1] in *Agkistrodon*, based on table 10.

Species	*bilineatus*	*piscivorus*	*blomhoffi*	*contortrix*	*halys*	*hypnale*	*rhodostoma*	*strauchi*	Number of characters shared by groups[2]
acutus	16-26[1] 61.5	17-26 65.4	14-26 53.8	15-26 57.7	7-20 35.0	15-26 57.7	9-16 56.3	8-16 50.0	
bilineatus		18-26 69.2	13-26 50.0	14-26 53.8	11-20 55.0	15-26 57.7	6-16 37.5	8-16 50.0	13-26 50.0
piscivorus			13-26 50.0	15-26 57.7	8-20 40.0	16-26 61.5	7-16 43.8	10-16 62.5	
blomhoffi				17-26 65.4	16-20 80.0	16-26 61.5	10-16 62.5	11-16 68.8	
contortrix					15-20 75.0	19-26 73.1	10-16 62.5	13-16 81.3	
halys						14-20 70.0	9-14 64.3	11-20 55.0	8-14 57.1
hypnale							10-16 62.5	11-17 64.7	
rhodostoma								9-13 69.2	

[1] Number of characters in common-number of characters used
per cent of characters in common.

[2] The New World forms of *Agkistrodon* share only 38.5 per cent (10 of 26) of characters; all members of the genus share 25.0 per cent (4 of 16) of characters.

On the basis of osteology, the *triseriatus* group of rattlesnakes is divided here into three subgroups. The most primitive of these seems to be the *intermedius* subgroup, which includes *intermedius* and *transversus*. Closely related is the *triseriatus* subgroup, which includes *pricei*, *triseriatus*, and *pusillus* (fig. 36). The third is the *lepidus* subgroup, which includes *lepidus* and *willardi*. The distinctness of these species and groups is supported by external morphology (H. M. Smith, 1946; Klauber, 1952, 1956). H. M. Smith (1946) separated *triseriatus* from *pricei*. H. M. Smith (1946) and Klauber (1952) separated *intermedius* (or its synonyms) and *transversus* from the other small crotalids and placed them in the *intermedius* group (*omiltemanus* subgroup of H. M. Smith, 1946). Unfortunately, the osteology of *intermedius* is known only from the figures and description in H. M. Smith (1946; listed as *C. gloydi lautus*), which show the pterygoid with a medial angle in the posterior third, the palatine low, and the anterior border of the splenial passing straight ventrally, posterior to the anterior Meckelian foramen. Little is known about *transversus*, as the species is known from only three preserved specimens. On the basis of color and scutellation, Klauber (1952) believed it to be most closely related to *intermedius*.

The shapes of the parietal, frontal, nasal, maxilla, and pterygoid suggest a close relationship of *pusillus* to *pricei* and *triseriatus*. It also has many characters in common with *C. willardi* and *S. ravus*. *Crotalus pusillus* is probably most closely related to *triseriatus*. *Crotalus pusillus* differs from *pricei* and *triseriatus* in that the basisphenoid has a well developed process with an anterior hump. This character may indicate a primitive relationship with *C. durissus* or with the primitive *Crotalus* stock.
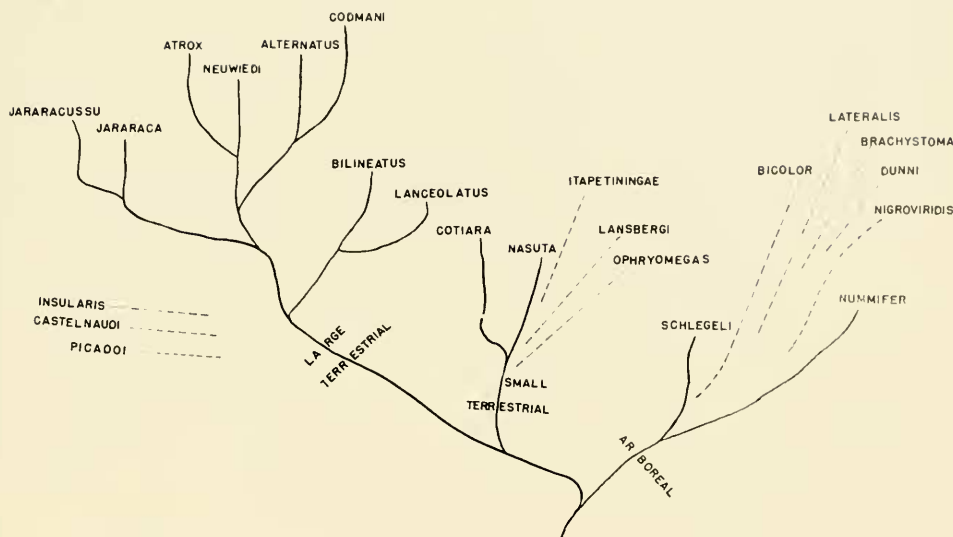
Fig. 35. Suggested phylogeny of *Bothrops*.

Crotalus lepidus is probably most closely related to *willardi*. This is suggested by the shape of the parietal, frontals, prefrontals, squamosals, pterygoids, and process of the basisphenoid. Both species have many characters in common with *C. triseriatus*, *C. pricei*, *S. catenatus*, and *S. miliarius* (fig. 36, tables 11, 14). *Crotalus lepidus* and *willardi* seem to form a subgroup related to the *triseriatus* subgroup.

The relationships of the forms within the *durissus* group (*horridus*, *molossus*, *basiliscus*, *durissus*, and *unicolor*) were first pointed out by Gloyd (1940). These relationships are supported by osteological evidence. *Crotalus horridus* and *molossus* are more closely related to each other than either is to the *basiliscus-durissus-unicolor* branch of the group.

Crotalus basiliscus is very closely related to *durissus*. The two differ in minor ways in the shapes of the prefrontal, palatines, etc. (table 11). They differ also in general body shape and in the height of the neural spines on the anterior vertebrae.

Crotalus d. unicolor van Lidth de Jeude, from Aruba Island, Dutch West Indies, has been considered both as a distinct species and as a subspecies of *durissus* (see Klauber, 1956: 44). The relationships are very close. Even though the material of *unicolor* examined consisted of young specimens, it was apparent that *unicolor* is more closely related to *C. d. terrificus* than to *C. d. tzabcan* on the basis of nasal and squamosal shape. For various reasons, Klauber (1956) and Gloyd (1940) kept *unicolor*, *tortugensis*, *exsul*, and *catalinensis* as distinct island species, even though their relationships to certain mainland species are apparent and close.

Gloyd (1940) and Klauber (1956) pointed out the distinctness of the *atrox* group of *Crotalus*. Both workers presented phylogenetic trees of this group. The osteological data support these suggested relationships. The *atrox* group includes *adamanteus* (with its Pleistocene clinal ancestor, *C. a. pleistofloridensis*) and the extinct *giganteus*. The group also includes *atrox* (with its island derivitive, *tortugensis*) and *ruber* (with its island derivitives, *exsul* and *catalinensis*). *Crotalus atrox* is intermediate in many osteological characters between *ruber* to the west and *adamanteus* to the east. *Crotalus atrox* is especially similar to *adamanteus* in frontal and parietal shape and to *ruber* in the shape of the basisphenoid, palatine, prefrontal, and ectopterygoid. Minton (1956) suggested, on the basis of venom, that *ruber* and *atrox* are closely related, showing less relationship to *adamanteus* than to each other, but within the

TABLE 14

Numerical summary of relationships[1] in *Crotalus* and *Sistrurus*, based on table 11.

Each cell gives: characters in common–characters used / per cent of characters in common.

Species	basiliscus	horridus	molossus	adamanteus	atrox	tortugensis	ruber	scutulatus	viridis	mitchelli	tigris	cerastes	enyo	lepidus	pricei	insertatus	willardi	pusillus	catenatus	miliarius	travus
durissus	23-29 / 79.3	18-29 / 62.1	23-29 / 79.3	17-29 / 58.6	20-29 / 69.0	17-27 / 63.0	17-29 / 58.6	16-29 / 55.2	10-29 / 34.5	14-29 / 48.3	12-29 / 41.4	12-29 / 41.4	10-29 / 34.5	13-29 / 44.8	12-29 / 41.4	13-26 / 50.0	11-29 / 37.9	19-29 / 65.5	17-29 / 58.6	12-24 / 50.0	17-27 / 63.0
basiliscus		20-29 / 69.0	21-29 / 72.4	20-29 / 69.0	17-29 / 58.6	16-27 / 59.3	13-29 / 44.8	16-29 / 55.2	11-29 / 37.9	13-29 / 44.8	13-29 / 44.8	12-29 / 41.4	9-29 / 31.0	14-29 / 48.3	11-29 / 37.9	11-26 / 42.3	12-29 / 41.4	19-29 / 65.5	17-29 / 58.6	13-24 / 54.2	17-27 / 63.0
horridus			23-29 / 79.3	18-29 / 62.1	17-29 / 58.6	15-27 / 55.6	16-29 / 55.2	17-29 / 58.6	17-29 / 58.6	13-29 / 44.8	19-29 / 65.5	16-29 / 55.2	17-29 / 58.6	15-29 / 51.7	17-29 / 58.6	18-26 / 69.2	18-29 / 62.1	16-29 / 55.2	16-29 / 55.2	13-24 / 54.2	16-27 / 59.3
molossus				22-29 / 75.9	17-29 / 58.6	16-27 / 59.3	18-29 / 62.1	13-29 / 44.8	11-29 / 37.9	16-29 / 55.2	12-29 / 41.4	11-29 / 37.9	11-29 / 37.9	11-29 / 37.9	10-29 / 34.5	13-26 / 50.0	13-29 / 44.8	15-29 / 51.7	13-29 / 44.8	11-24 / 45.8	12-27 / 44.4
adamanteus					24-29 / 82.8	17-27 / 63.0	18-29 / 62.1	12-29 / 41.4	14-29 / 48.3	16-29 / 55.2	12-29 / 41.4	12-29 / 41.4	12-29 / 41.4	11-29 / 37.9	12-29 / 41.4	10-26 / 38.5	17-29 / 58.6	14-29 / 48.3	18-29 / 62.1	12-24 / 50.0	13-27 / 48.1
atrox						15-27 / 55.6	22-29 / 75.9	11-29 / 37.9	14-29 / 48.3	14-29 / 48.3	13-29 / 44.8	13-29 / 44.8	13-29 / 44.8	12-29 / 41.4	14-29 / 48.3	10-26 / 38.5	14-29 / 48.3	12-29 / 41.4	14-29 / 48.3	9-24 / 37.5	12-27 / 44.4
tortugensis							18-27 / 66.7	17-27 / 63.0	17-27 / 63.0	16-27 / 59.3	16-27 / 59.3	16-27 / 59.3	16-27 / 59.3	18-27 / 66.7	18-27 / 66.7	17-27 / 63.0	19-27 / 70.4	18-27 / 66.7	21-27 / 77.8	18-22 / 81.8	20-27 / 74.1
ruber								15-29 / 51.7	19-29 / 65.5	16-29 / 55.2	18-29 / 62.1	17-29 / 58.6	16-29 / 55.2	14-29 / 48.3	16-29 / 55.2	14-27 / 51.9	15-29 / 51.7	12-29 / 41.4	16-29 / 55.2	12-24 / 50.0	15-27 / 55.6
scutulatus									19-29 / 65.5	17-29 / 58.6	20-29 / 69.0	20-29 / 69.0	18-29 / 62.1	18-29 / 62.1	16-29 / 55.2	16-27 / 59.3	15-29 / 51.7	14-29 / 48.3	18-29 / 62.1	14-24 / 58.3	19-27 / 70.4
viridis										18-29 / 62.1	18-29 / 62.1	23-29 / 79.3	24-29 / 82.8	16-29 / 55.2	18-29 / 62.1	17-27 / 63.0	22-29 / 75.9	14-29 / 48.3	18-29 / 62.1	15-24 / 62.5	16-27 / 59.3
mitchelli											17-29 / 58.6	18-29 / 62.1	16-29 / 55.2	13-29 / 44.8	10-29 / 34.5	12-27 / 44.4	12-29 / 41.4	14-29 / 48.3	14-29 / 48.3	11-24 / 45.8	15-27 / 55.6
tigris												25-29 / 86.2	16-29 / 55.2	19-29 / 65.5	21-29 / 72.4	18-27 / 66.7	20-29 / 69.0	13-29 / 44.8	18-29 / 62.1	15-24 / 62.5	15-27 / 55.6
cerastes													22-29 / 75.9	20-29 / 69.0	21-29 / 72.4	19-27 / 70.4	18-29 / 62.7	14-29 / 48.3	18-29 / 62.1	15-24 / 62.5	15-27 / 55.6
enyo														17-29 / 58.6	20-29 / 69.0	19-27 / 70.4	20-29 / 69.0	15-29 / 51.7	17-29 / 58.6	14-24 / 58.3	14-27 / 51.9
lepidus															21-29 / 72.4	16-27 / 59.3	18-29 / 62.1	17-29 / 58.6	19-29 / 65.5	17-24 / 70.8	18-27 / 66.7
pricei																18-27 / 66.7	19-29 / 65.5	14-29 / 48.3	19-29 / 65.5	16-25 / 66.7	18-27 / 66.7
triseriatus																	19-26 / 73.1	16-26 / 61.5	17-26 / 65.4	15-21 / 71.4	15-24 / 62.5
willardi																		19-29 / 65.5	23-29 / 79.3	19-24 / 79.2	16-27 / 59.3
pusillus																			21-29 / 72.4	19-24 / 79.2	19-27 / 70.4
catenatus																				21-24 / 87.5	21-27 / 77.8
miliarius																					16-22 / 72.7

Number of characters shared by group enclosed[2]

- 3-29 / 10.2
- 8-29 / 27.6
- 8-29 / 27.6
- 12-29 / 41.4
- 9-26 / 34.6
- 12-29 / 41.4

[1] Number of characters in common–number of characters used / per cent of characters in common.

[2] *durissus* and *triseriatus* groups: 5-29, 17.5; *durissus* and *Sistrurus* groups: 9-29, 31.0.
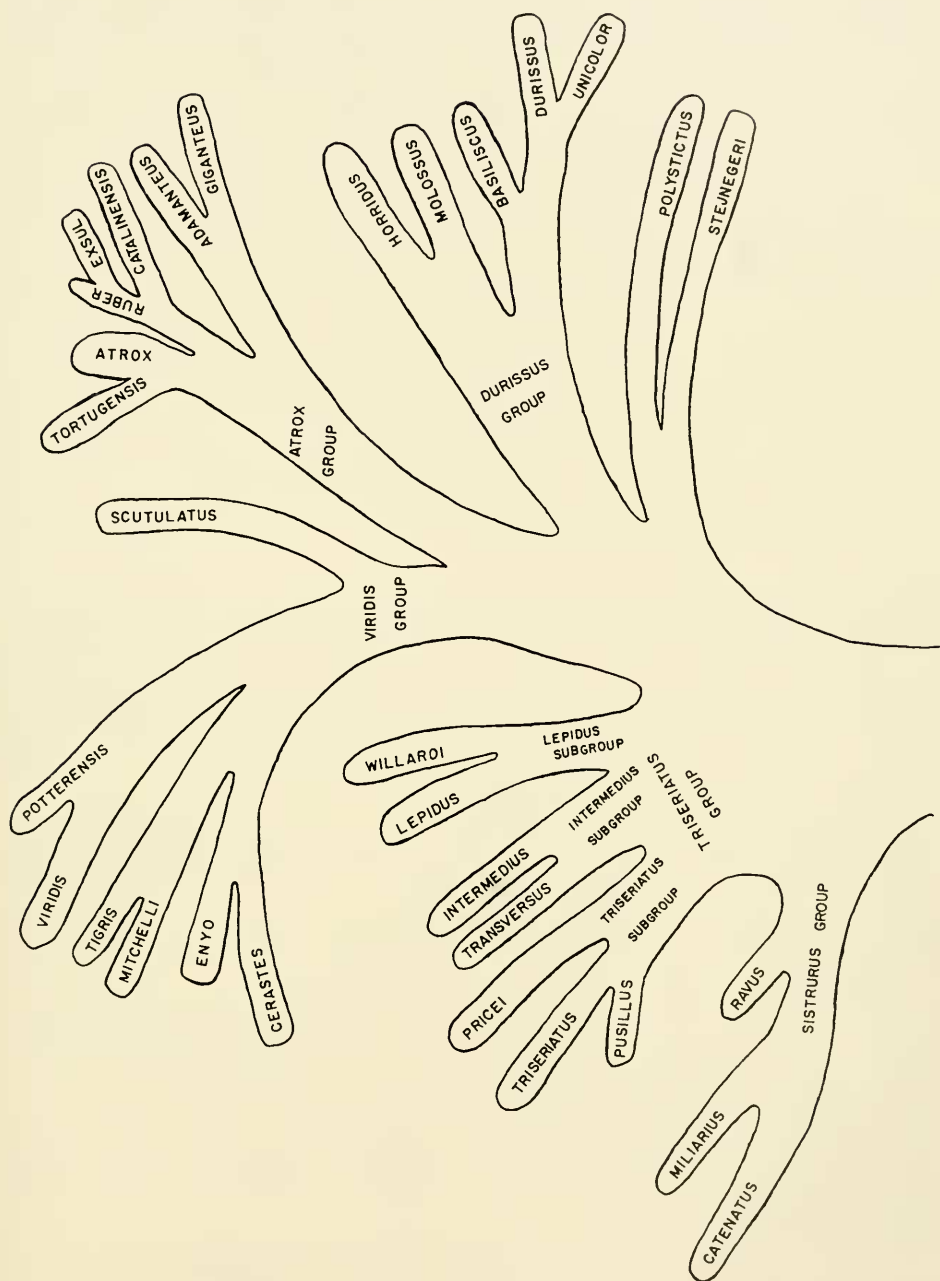
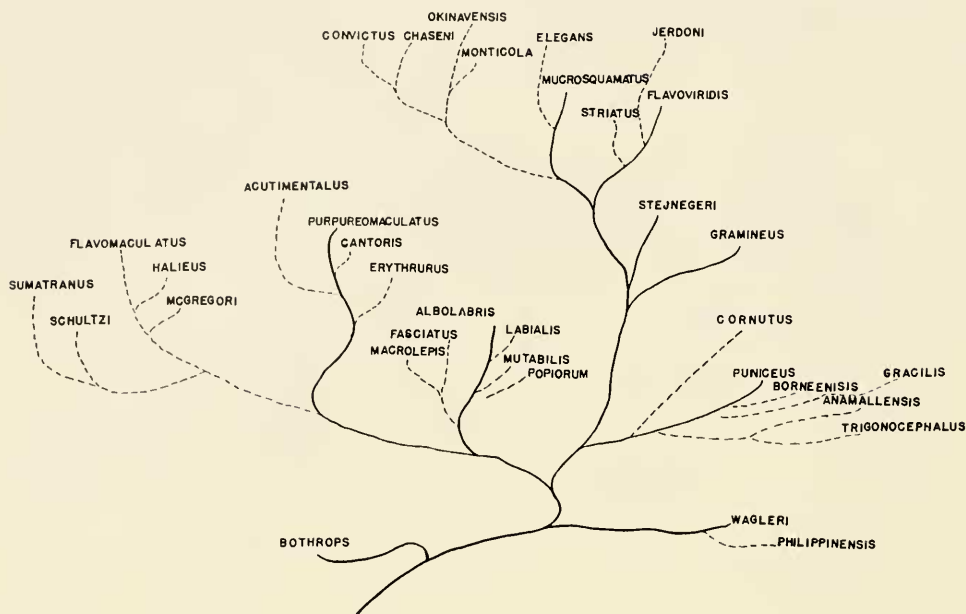Fig. 36. Suggested phylogeny of *Crotalus*, including *Sistrurus*.

Fig. 37. Suggested phylogeny of *Trimeresurus*. Solid lines, species examined osteologically; dashed lines, species known only from external characters, largely from Maslin, 1942.

same venom group. *Crotalus adamanteus* has the most specialized venom of the three species. On the basis of both osteology and external morphology, *tortugensis* appears to be a small form of *atrox*. *Crotalus tortugensis* resembles *ruber* in one peculiar character, having a ventrally-turned anterolateral process on the ectopterygoid.

Crotalus exsul from Cedros Island, Baja California, is so closely related to *ruber* that if it were not for complicated nomenclatorial changes the two forms would probably be considered subspecific by most people. No skeletons were seen of *exsul* or of the recently described *catalinensis* Cliff from Catalina Island, Gulf of California, Mexico, but the relationships of *exsul* to *C. r. ruber* and of *catalinensis* to *C. r. lucasensis* are so close on the basis of external characters that the osteology probably does not differ greatly.

The relationship of *scutulatus* has been assumed to be with the *atrox* group, but *scutulatus* differs from that group in many respects, as noted by Klauber (1930). The venom and certain head scales suggest relationships with *durissus*. Klauber (1930, 1956) and Gloyd (1940) considered *scutulatus* intermediate between the *atrox* and *viridis* groups. On the basis of its osteology, especially the shapes of the parietal, frontal, maxilla, and basisphenoid (table 11), *scutulatus* appears to be very closely related to the *viridis* group. It retains some of the primitive scale characters of the genus *Crotalus* and of the *atrox* group. The species probably represents an early offshoot of the *viridis* group, soon after the differentiation of the *viridis* and *atrox* groups (fig. 36).

The *viridis group*, as here defined, includes *mitchelli, tigris, viridis, cerastes, enyo*, and *potterensis*. These forms have 14 of 29 characters (48.3 per cent) in common. They are especially similar in frontal and parietal shape. They each have an anteriorly directed depression posterior to the process in the curvature of the pit-cavity of the maxilla. They all have relatively simple prefrontals and (except for *mitchelli*) low basisphenoids. The relationships of these species were first noted by Amaral (1929). Gloyd (1940) considered the relationship of

enyo, cerastes, and *tigris* unknown. Klauber (1956) placed *mitchelli, tigris,* and *viridis* close together, but considered the relationship of *cerastes* and *enyo* to be with *durissus* (see discussion below).

The most divergent member of the *viridis* group is *mitchelli.* In the shape of the processes of the prefrontal and in the well-developed process of the basisphenoid, it resembles the *atrox* and *durissus* groups. *Crotalus mitchelli* is probably the most primitive member of the *viridis* group, *i.e.,* it has changed least from the main *Crotalus* stock. This view is suggested by the shape of the basisphenoid and prefrontal and by the configuration of certain head scales.

Osteologically, *viridis* seems to be closely related to *potterensis, tigris,* and *enyo* (table 14). On the basis of osteology, intraspecific relationships in *viridis* are difficult to determine. *Crotalus v. concolor* and *C. v. lutosus* seem closely related, as do *C. v. helleri* and *C. v. oreganus.* In many characters, however, *C. v. oreganus* is more like *C. v. viridis* than like either *C. v. lutosus* or *C. v. helleri.*

Crotalus potterensis is an extinct fossil species of the *viridis* group, described by Brattstrom (1953) from the Pleistocene of Potter Creek Cave, Shasta County, California, on the basis of two vertebrae, a part of a pterygoid, ribs, and other fragments. Subsequently, many other vertebrae from the same locality have been found in the paleontological collections of the University of California at Berkeley. This new material shows a change through time from typical *viridis* to typical *potterensis* within the cave deposits (Brattstrom, 1958). *Crotalus potterensis* differs from *viridis* in several characters, such as larger size and greater centrum length and diameter; they are similar in shape of the pterygoid and number of pterygoid teeth.

As noted above, the relationships of *cerastes* and *enyo* have been uncertain (Amaral, 1929; Gloyd, 1940; Klauber, 1956). It is suggested here that *cerastes* and *enyo* are members of the *viridis* group in view of the deep anteriorly-directed depression in the pit-cavity curvature, the low basisphenoid, the elongate frontals, etc. (tables 11, 14). On the basis of some minor hemipenal characters, the prominent scale tuberculations, and a high neural spine, Klauber (1956) suggested that *cerastes* and *enyo* are related to *durissus.* The hemipenal characters are also shared with such species as *adamanteus* and *pricei.* Klauber (1936b) had previously noted the scale and color similarities of *cerastes* and *mitchelli.*

A high neural spine is found on the anterior vertebrae of *durissus* (fig. 11), *cerastes,* and *enyo,* as pointed out by Klauber (1956), but I believe that the similarity results from convergence. In *durissus* the high neural spine accounts for the high dorsal ridge evident externally. This ridge may be associated with the method of forming the resting coil in which each upper body loop is placed partly on the lower body loop rather than flat on the ground as in other species, or it may be associated with the peculiar striking position taken by this species. A very low neural spine is found in *basiliscus* (table 8), which is extremely similar to *durissus* in scutellation and in most osteological characters examined. *Crotalus basiliscus* differs from *durissus* externally primarily in being an extremely heavy flat snake; as far as known it does not coil or strike like *durissus.*

In *cerastes* and *enyo* the tall neural spine is only slightly evident as a ridge externally. Here the tall neural spine may be primarily associated with increased musculature in the anterior thoracic region, used in the lateral undulations of *enyo* and the sidewinding locomotion of *cerastes.* Both species occur typically in open desert areas. The high neural spine in *cerastes* and *enyo* might represent an increased area for muscle attachment permitting fast movements across open areas (Cowles, 1956), with *cerastes* using an additional, more elaborate, mechanism — sidewinding. It is thus probable that the high neural spine has evolved twice in *Crotalus* for two separate functions and does not indicate, as Klauber (1956) believed, a relationship of *cerastes* and *enyo* to *durissus.*

Crotalus cerastes and *enyo* are similar to the *viridis* group in external characters (Amaral, 1929), in venom characters (Minton, 1956), and in skeletal characters (tables 11, 14). *Crotalus cerastes* and *enyo* have 70 to 86 per cent of their skeletal characters in common with members of the *viridis* group, and only 41 to 45 per cent in common with *durissus.*

TABLE 15

Numerical summary of relationships[1] in *Bothrops*, based on table 12.

Species	atrox	bilineatus	godmani	jararaca	jararacussu	lanceolatus	neuwiedi	cotiara	nasuta	nummifer	schlegeli
alternatus	18-24 75.0	16-21 76.2	13-20 65.0	18-24 75.0	18-24 75.0	16-24 66.7	16-24 66.7	16-22 72.7	8-13 61.5	10-22 45.5	12-23 52.2
atrox		14-22 63.6	11-18 61.6	17-25 68.0	18-25 72.0	18-25 72.0	16-25 64.0	15-23 65.2	7-13 53.8	10-23 43.4	8-24 33.3
bilineatus			11-19 57.9	16-22 72.7	12-22 54.4	13-22 59.1	11-22 50.0	14-20 70.0	5-13 38.5	9-20 45.0	11-21 52.4
godmani				14-20 70.0	11-20 55.0	11-20 55.0	16-20 80.0	12-18 66.7	9-12 75.0	11-18 61.1	11-19 57.9
jararaca					17-25 68.0	16-25 64.0	16-25 64.0	15-23 65.2	9-13 69.2	11-23 47.8	13-24 54.2
jararacussu						20-25 80.0	15-25 60.0	13-23 56.5	8-13 61.5	10-23 43.5	8-24 33.3
lanceolatus							17-25 68.0	15-23 65.2	8-13 61.5	8-23 34.8	8-24 33.3
neuwiedi								17-23 73.9	8-13 61.5	13-23 56.5	11-24 45.8
cotiara									6-11 54.5	10-21 47.6	10-23 43.5
nasuta										7-13 53.8	4-12 33.3
nummifer											14-22 63.6

[1]Number of characters in common-number of characters used
  per cent of characters in common.

PHYLOGENY OF *BOTHROPS*

The relationships of the species within the genus *Bothrops* are poorly known. About 30 or 40 species have been described in the genus, of which probably two-thirds are valid. Many species are known from only one or two specimens each. Because of the lack of material, only a few species have been examined in this study (table 2). It is hoped that the separation of the major groups and subgroups of *Bothrops* on the basis of osteology will aid further systematic work.

As noted above and in figure 35, the genus *Bothrops* is divisable into two major groups based on osteology and scutellation. One of the groups is here termed the "arboreal" group, though not all members are arboreal; it includes at least *nummifer* and *schlegeli*. These two species are very much alike in the shapes of the frontal, parietal, lower jaw, palatine, ectopterygoid, and premaxilla. Both appear to be quite primitive, with *schlegeli* probably the most primitive member of the genus. As noted above, *schlegeli* has several characters in common with the unique *Trimeresurus wagleri*. *Bothrops schlegeli* and *T. wagleri* probably have changed very little since their differentiation from the main lines of evolution of their respective genera. To judge from scutellation and habit, *B. bicolor, lateralis, brachystoma, dunni,* and *nigroviridis* may be related to *nummifer* and *schlegeli* (fig. 35).

TABLE 16

Numerical summary of relationships[1] in *Trimeresurus* and *Bothrops*, based on table 12.

Species	T. flaviviridis	T. mucrosquamatus	T. puniceus	T. purpureomaculatus	T. stejnegeri	T. wagleri	B. atrox	B. nummifer
T. gramineus	13-26 50.0	4-13 30.8	9-15 60.0	13-26 50.0	8-14 57.1	10-26 38.5	6-26 23.1	8-23 34.8
T. flaviviridis		5-13 38.5	8-15 53.3	13-26 50.0	7-14 50.0	11-26 42.3	12-26 46.2	8-23 34.8
T. muscrosquamatus			2-7 28.6	7-13 53.8	8-9 88.9	5-13 38.5	8-13 61.5	8-13 61.5
T. puniceus				9-15 60.0	4-9 44.4	7-14 50.0	3-15 20.0	7-14 50.0
T. purpureomaculatus					9-14 64.3	12-26 46.2	10-26 38.5	15-23 65.2
T. stejnegeri						6-14 42.9	5-14 35.7	8-14 57.1
T. wagleri							9-26 34.6	14-23 60.9
B. atrox								10-23 43.5

[1]Number of characters in common-number of characters used
per cent of characters in common.

The second group is here called the "terrestrial" group, although a few members are somewhat arboreal. This group includes two subgroups, the small "hog-nosed pit vipers" and the large terrestrial forms. The first subgroup includes *cotiara* and *nasuta*, which have several characters in common (tables 12, 15). To judge from external characters, this group may also include *lansbergi, itapetiningae,* and *ophryomegas* (fig. 35).

The subgroup of large terrestrial forms of *Bothrops* includes *jararaca, jararacussu, atrox, neuwiedi, godmani, alternatus, bilineatus,* and *lanceolatus. Bothrops insularis, castelnaudi,* and *picadoi* also may belong here, to judge from external characters. These species all seem closely related. The number of characters each has in common with other members of its genus can be seen in table 15. As most of the species have not been examined osteologically, the relationships diagrammed (fig. 35) are highly tentative.

PHYLOGENY OF *TRIMERESURUS*

Only seven species of this large genus have been examined osteologically. Contributions to our knowledge of relationships within this genus have been made by Pope and Pope (1933), Pope (1935), and Maslin (1942). The taxonomic status of many of the species of *Trimeresurus* is still, however, in doubt. This is due to the absence of adequate distributional and ecological data as well as to the paucity of specimens. Fortunately, specimens were examined of species representative of most of the groups of *Trimeresurus* of Maslin (1942).

As has been mentioned several times above, *T. wagleri* is the most distinct species in the Crotalidae. It has many characters that distinguish it not only from other species of *Trimeresurus* but also from most other crotalids; these include the medial location of the lower lumen of the fang, the depressed centers of the frontals, the low palatine, and the shape of the postfrontal, lower jaw, and ectopterygoid. In skull type, *wagleri* probably approaches the Viperidae more closely than does any other crotalid, and in this way it is probably the most primitive member of the family. Even though it may have retained many of the primitive characters of the family, however, it is highly specialized in other characters, such as its depressed frontals and medial lower lumen of the fang. Because of its differences, *wagleri* is here separated from the other species of *Trimeresurus* into a distinct subgenus, for which the name *Tropidolaemus* Wagler is available. The very similar and probably subspecific (see E. H. Taylor, 1922) form, *T. philippinensis*, is included with it in this subgenus. No skulls of *T. philippinensis* were examined.

Table 16 shows the number of characters each member of the genus has in common with each other member. *Trimeresurus stejnegeri* appears similar in many respects to *gramineus* and *puniceus*. The most striking osteological similarity is in parietal shape. Maslin (1942) placed *stejnegeri* in the same group as *gramineus*. The *puniceus* group of Maslin (1942) includes *puniceus*, *gracilis*, *borneensis*, *cornutus*, *anamallensis*, and *trigonocephalus*. Osteologically, *T. puniceus* appears to be related to a primitive *gramineus-stejnegeri* as evidenced by the shapes of its parietal, frontal, and maxilla. The presence of the anterior hump on the basisphenoid in *flaviviridis* and *puniceus* may be due to convergence or may indicate some relationship.

Trimeresurus mucrosquamatus is similar in many respects to *flaviviridis*, *stejnegeri*, and *gramineus*. Maslin (1942) placed it in a group with *elegans*. *Trimeresurus purpureomaculatus* is similar to *stejnegeri* in the shapes of frontal and basisphenoid and to *gramineus* in the shapes of pterygoid, maxilla, and parietal. Maslin (1942) included *purpureomaculatus* in a group with *acutimentalis* and *erythrurus*. The reduction of palatine and pterygoid teeth indicates, along with scutellation and characters of the basisphenoid and ectopterygoid, that *flaviviridis* is quite specialized. This specialization is probably related to its isolation on the Ryukyu Islands. Maslin (1942) placed *flaviviridis* in a group with *jerdoni*, which also lacks palatine teeth. Osteologically, *flaviviridis* seems to be related to a primitive *mucrosquamatus-stejnegeri-gramineus* stock, as indicated by the shapes of the frontal, parietal, postfrontal, and basisphenoid.

Figure 37 presents a very tentative suggestion of relationships within the genus *Trimeresurus*. The probable phylogenetic positions of members of the genus that were not studied osteologically are included from the information presented by Maslin (1942). The position of *wagleri* and its related form is well documented. On the basis of both osteological and external characters, the relationship among the *monticola*, *mucrosquamatus*, *jerdoni*, and *flaviviridis* groups and their position relative to *stejnegeri* and *gramineus* seem fairly well established. These groups also show a similarity in that the hemipenes bear true spines, lacking in other members of the genus (Maslin, 1942). The position of the other forms in the genus is quite tentative.

Taxonomy

In view of the relationships suggested above on the basis of osteology and supported by evidence from the study of scutellation, venoms, hemipenes, and hybridization, a few taxonomic changes seem necessary. These changes are primarily associated with the use of the subgeneric concept. Though the subgenus is seldom used in modern herpetology, it is my opinion that it is useful in indicating relationships within a genus. For this reason, the two basic groups of *Trimeresurus* are separated as subgenera: *wagleri* and *philippinensis* are placed in *Tropidolaemus* Wagler, and the remaining species in the nominate subgenus. It is also suggested that the two basic groups in the genus *Bothrops* should be treated as subgenera: *Bothrops* and *Bothriechis*, the latter to include the so-called "arboreal" group of species.

It has been noted that the characters of the genera *Crotalus* and *Sistrurus* merge or break down. This breakdown is especially true in the *Sistrurus-C. triseriatus* complex, as seen in the osteology, hemipenes, squamation, venoms, and color. Also, hybridization occurs. It is my belief that the differences between *Crotalus* and *Sistrurus* are best indicated by placing all the rattlesnakes in one genus and considering *Sistrurus* as a subgenus. More than likely, for purposes of stability, most modern herpetologists will not readily take up *Sistrurus* as a subgeneric name. This is not really important as long as it is realized that the difference between *Sistrurus* and *Crotalus* is almost of the same order of magnitude as that between other species groups within *Crotalus*.

Because of the seemingly different directions of evolution, the development of the loreal pit in the Crotalidae, and their geographic distribution, it is desirable that the Viperidae and Crotalidae be given full family rank, as has been done by various authors (Gilmore, 1938; Klauber, 1936a; H. M. Smith, 1950; Brattstrom, 1954).

In the past, when the Crotalidae has been given family rank, two subfamilies have often been designated: the Lachesinae, including *Lachesis, Bothrops, Trimeresurus*, and sometimes *Agkistrodon* (Amaral, 1938), and the Crotalinae, including *Crotalus* and *Sistrurus*. This subfamily arrangement is untenable in view of the relationships of *Lachesis* to *Crotalus* suggested above and in view of the supposedly primitive condition of *Agkistrodon*. The only logical suprageneric grouping would place *Bothrops* and *Trimeresurus* in one group and *Agkistrodon, Crotalus*, and *Lachesis* in another. However, in my opinion, the division of the Crotalidae into subfamilies does not clarify any relationships and would be highly artificial.

A summary of the generic and subgeneric taxonomy of the Crotalidae is given below. The characteristics of each genus and subgenus are listed, as well as the forms included in the taxa as here defined. No attempt has been made to give complete synonymies of the taxa, as these can be found in Gloyd (1940), Gloyd and Conant (1943), Klauber (1936b, 1952, 1956), Maslin (1942), Smith and Taylor (1945), and M. A. Smith (1943).

Family CROTALIDAE Gray
Genus **Agkistrodon** Beauvois

Genotype. — *Cenchris mokeson* (Daudin).

Characteristics. — Top of head with large plates anteriorly, usually nine in number. Subcaudals in one or two rows. Pterygoid teeth extending posteriorly past middle of junction of ectopterygoid. Ectopterygoid usually shorter than basal portion of pterygoid. Frontals flat or turned up laterally. Palatine with a dorsal hump. Curvature of pit cavity a simple, open curve.

Range. — United States, Mexico, Central America, southeastern Asia to southeastern Europe.

Referred species. — *acutus, annamensis, bilineatus, blomhoffi, contortrix, halys, himalayanus, hypnale, millardi, mokeson, monticola, nepa, piscivorus, rhodostoma, strauchi.*

Genus **Bothrops** Wagler
Subgenus **Bothrops** Wagler

Genotype. — *Coluber lanceolatus* Lacépède.

Characteristics. — Top of head with numerous small scales of varying size, including several scales in frontal area. Head scales usually keeled; gular scales not keeled. Subcaudals in one or two rows. Pterygoid teeth extending posteriorly past middle of articulation of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Palatine forked anteriorly. Postnasal pore usually absent. Frontals flat or turned up laterally, longer than wide. Edge of pit cavity with a smooth curve. Primarily terrestrial.

Range. — Mexico, Central and South America.

Referred species. — *alternatus, atrox, bilineatus, godmani, insularis, jararaca, jararacussu, lanceolatus, neuwiedi.* The species *cotiara, lansbergi, nasuta, ophryomegas, picadoi,* and other little-known species of *Bothrops* may belong here, or they may represent additional subgenera.

Subgenus **Bothriechis** Peters

Genotype. — *Bothriechis nigroviridis* Peters.

Characteristics. — Like the above except palatine (roundish) not forked anteriorly; frontal wider than long; curvature of pit cavity sometimes with a median hump. Usually arboreal.

Range. — Mexico, Central and South America.

Referred species. — *bicolor, brachystoma, dunni, lateralis, nigroviridis, nummifer,* and *schlegeli.* Probably some of the other little-known arboreal species of *Bothrops* belong here, but they are not assigned to either subgenus for lack of information. The name *Teleuraspis* Cope, (Proc. Acad. Nat. Sci. Philadelphia, 1859:338, Type *Trigonocephalus schlegeli* Berthold) is available if the arboreal group of *Bothrops* is further divided in the future.

Genus **Crotalus** Linnaeus
Subgenus **Crotalus** Linnaeus

Genotype. — *Crotalus horridus* Linnaeus.

Characteristics. — Top of head with scales of varying size; more than one scale in frontal area. Parietal scales, if enlarged, not in contact nor symmetrical. Rattles present. Subcaudals in one or two rows. Pterygoid teeth not extending posteriorly past middle of articulation of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Frontals flat or turned up laterally. Curvature of pit cavity interrupted by a dorsal hump or process. Lateral process of squamosal blunt or pointed, but if forming a fork with the main bone, angle between them 90° or greater.

Range. — North, Central, and South America.

Referred species. — *adamanteus, atrox, basiliscus, catalinensis, cerastes, durissus, enyo, exsul, horridus, intermedius, lepidus, mitchelli, molossus, polystictus, pricei, pusillus, ruber, scutulatus, stejnegeri, tigris, tortugensis, transversus, unicolor, viridis, willardi,* †*potterensis,* †*giganteus.*

Subgenus **Sistrurus** Garman

Genotype. — *Crotalus miliarius* Linnaeus.

Characteristics. — Top of head with large plates anteriorly, usually nine in number, including a single frontal and a pair of large symmetrical parietals in contact. Rattles present. Subcaudals in one or two rows. Pterygoid teeth not extending past middle of articulation of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Frontals flat or turned up laterally. Curvature of pit cavity interrupted by a dorsal hump or process. Lateral process of squamosal forked at an angle of 80° or less with the main bone, except in *C. ravus.*

Range. — Eastern Canada, eastern United States, and central Mexico.

Referred species. — *catenatus, miliarius, ravus.*

Genus **Lachesis** Daudin

Genotype. — *Crotalus mutus* Linnaeus.

Characteristics. — Top of head with small, keeled scales. Posterior subcaudals in four rows. Pterygoid teeth not extending posteriorly past middle of junction of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Palatine with high dorsal hump. Top of frontals flat. Curvature of pit cavity interrupted by a well-developed process with a small depression on its outer surface.

Range. — Central and northern South America, Trinidad Island.

Referred species. — *muta.*

Genus **Trimeresurus** Lacépède
Subgenus **Trimeresurus** Lacépède

Genotype. — *Trimeresurus viridis* Lacépède (= *T. gramineus* (Shaw)).

Characteristics. — Top of head with numerous small scales of varying size, including several or many scales in the frontal area. Nasal pore usually present on posterior wall of nostril.

Scales on top of head anterior to parietal region smooth; gular scales not keeled. Subcaudals in one or two rows. Pterygoid teeth extending posteriorly beyond middle of articulation of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Palatine not forked anteriorly. Frontals flat or at least without depressed centers. Lower lumen of fang anterior. Prefrontal laterally longer than wide. Curvature of pit cavity having a small hump or process. Gular scales not keeled. Venom, as far as known, hemotoxic. Terrestrial or arboreal.

Range. — Southeastern Asia to India and Ceylon.

Referred species. — *acutimentalis, albolabris, anamallensis, borneensis, cantoris, chaseni, convictus, cornutus, elegans, erythrurus, fasciatus, flavomaculatus, flavoviridis, gracilis, gramineus, halieus, jerdoni, kanburiensis, kaulbacki, labialis, macrolepis, malabaricus, mcgregori, monticola, mucrosquamatus, mutabilis, okinavensis, popiorum, puniceus, purpureomaculatus, schultzi, stejnegeri, strigatus, sumatranus, trigonocephalus.*

Subgenus **Tropidolaemus** Wagler

Genotype. — *Cophias wagleri* Boie.

Characteristics. — Top of head with numerous small scales of varying size, including many or several in the frontal area. All scales on top of head usually keeled; gular scales keeled. Nasal pore absent. Subcaudals in one or two rows. Pterygoid teeth extending posteriorly past middle of junction of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Palatine low, not humped or forked. Frontals with centers depressed. Lower lumen of fang medial. Prefrontals laterally wider than long. Curvature of pit cavity interrupted by a small process or knob. Venom neurotoxic. Color primarily green. Arboreal.

Range. — Malaya, Sumatra, Philippine Islands.

Referred species. — *wagleri* and probably *philippinensis.* The latter was not seen, but was considered by Taylor (1922) to be very closely related to *wagleri*, if not subspecific.

ZOOGEOGRAPHY

After the basic relationships for a group have been established, it is interesting and enjoyable to speculate on the evolution and zoogeography of the group.

Darlington (1957) recently summarized the zoogeography of the pit vipers as follows: "Crotalines are unknown fossil before the Pliocene (when rattlesnakes were in North America). Other clues suggest that the subfamily originated in Asia and that both *Agkistrodon* and *Trimeresurus* (*Bothrops*) moved from Asia to America, one of these general [*sic*] (or an earlier stock) presumably giving rise to the rattlesnakes" (p. 228), and ". . . pit-vipers probably arose (from true vipers) in southern Eurasia, and two or three stocks reached America, one producing the rattlesnakes" (p. 203-204).

As will be seen below, I do not disagree with this interpretation but wish only to expand the discussion. Someone has said that all zoogeography is speculation. I do not agree completely, but it must be realized that the following comments are largely that. It is my interpretation of events which may have taken place if the data on the fossils and phylogeny are accurate and the basic assumptions are correct.

For an evolutionary and zoogeographic analysis, something should be known of (1) the relationships of the species and genera, (2) the fossil history, (3) the ecology, behavior, and physiology of recent forms, (4) the distribution of land areas and bridges at various times in the past, and (5) past climatic conditions.

Phylogeny and fossils. — The relationships and phylogeny of the pit vipers are summarized in figures 33 to 37 and tables 13 to 16. Fossil crotalids do not aid greatly in interpreting relationships or in constructing past distributions. Many recent species have changed little since the Pliocene (Brattstrom, 1954; Klauber, 1956).

Land areas and bridges. — The distribution of the continents during the history of the Crotalidae has probably been similar to that of today. Theories for Cenozoic and Mesozoic continental drift and trans-oceanic land bridges (between South America and Africa and between South America and Asia) have been discarded by most workers (Mayr *et. al.*, 1952;

Press *in* Poldervaart *et al.*, 1955). The presence and absence of certain island chains are of critical importance in interpreting zoogeographic distribution. In regard to the history of the Crotalidae, the North and South American connections, the Bering land bridge, and the changes in the Sundaland islands are extensively documented and discussed in the literature (Underwood, 1954; Inger, 1947, 1954; Hesse, Allee, and Schmidt, 1951; Darlington, 1948, 1957; Simpson, 1947, 1953, 1956; Stirton, 1950; Durham, Arellano, and Peck, 1955). These data will not be reviewed here but will be taken into consideration in the speculations to be presented. For example, a group is not stated as having dispersed to a certain area until a land bridge is inferred to have been present.

The possibility of chance dispersal on rafts, etc., (Simpson, 1952, 1953, 1956; Axelrod, 1952b) is probably not of major importance in crotalid zoogeography. No crotalids occur in the West Indies, the Galapagos or Revillagigedos islands, New Guinea, Australia, Celebes, or the islands of Oceania. The possibility of rafting is not entirely ruled out, however, and there are even records of *Crotalus adamanteus* swimming 22 miles out to sea between the Florida Keys (Klauber, 1956: 464, 470). The swimming ability of other crotalids is also documented (Klauber, 1956: 464-472). Though the distribution of crotalids in the Malaya-Borneo-Philippine area is primarily associated with Sundaland (Darlington, 1948) or other known land bridges (see Inger, 1947, 1954, for discussion and review), there remains a possibility of crotalids having rafted to some of these islands, or across the Bering and Panama sea straits, cr to the islands of Trinidad, Martinique, or Formosa.

Chance dispersal by crotalids on rafts would be facilitated by their being ectothermic. In a cool area they would be able to withstand long periods without food. Rafting in cold areas, however, would probably be lethal to the snakes (Brattstrom, MS; Klauber, 1956: 387-391).

Ecology of recent forms. — The temperature requirements of a few crotalids are relatively well known (Cowles and Bogert, 1944; Cowles, 1945; Fitch, 1960; Brattstrom, MS). As ectothermic reptiles, their body heat comes entirely from external sources (Cowles and Bogert, 1944; Brattstrom, MS). As noted by Cowles (1945) and correlated with Bergmann's rule for ectotherms, large ectotherms do not live in more northern latitudes today. This is largely because in more northern latitudes there is not enough solar radiation (the major source of heat to ectotherms) to heat a large reptile to body temperatures under which it can carry out its normal physiological and ecological functions. Small lizards and snakes (*Eumeces, Thamnophis*) and frogs, toads, and salamanders (with their lower thermal preferences) can and do occur in northern latitudes today. Cold or cool northern climates apparently inhibit the northern distribution of crotalids. This is of importance in interpreting the zoogeography cf the crotalids, especially in regard to the times of dispersal across the Bering land bridge. For example, though such warm-blooded forms as horses, mammoths, and mastodons could cross the Bering land bridge during the cold periods of the Pleistocene (Simpson, 1947; Stirton, 1950), probably the cold Pleistocene glacial climates and probably even the cool interglacial climates, if they were similar to that of today, inhibited dispersal of crotalids across the Bering land bridge.

The present distribution of the Crotalids is shown in figure 38, and the present distribution of the various genera in figures 40C and 41. Except for *Crotalus* and *Sistrurus* (Klauber, 1956) and the copperheads (Fitch, 1960), the ecology of most crotalids is not well documented. *Trimeresurus* and *Bothrops* are tropical today, *Trimeresurus* in southeastern Asia and the Sundaland, Philippine, and Ryukyu islands, *Bothrops* in Central and South America. *Agkistrodon* is primarily warm temperate. *Agkistrodon contortrix* is primarily associated with the Eastern Deciduous Forest, occurring rarely into semiarid areas in Texas. The semiaquatic *A. piscivorus* occurs in the warm temperate to subtropical areas of the southeastern United States. *Agkistrodon bilineatus*, though occurring within the tropical region, is apparently primarily associated with temperate climates. The ecology of the Asiatic forms of *Agkistrodon* is not well known, but apparently most occur in temperate climates, often in relatively cool montane regions within the tropics; hence the apparent overlap in range of *Trimeresurus* and

Agkistrodon (fig. 40C). *Lachesis muta* occurs today in the tropical regions of southern Central and northern South America and in Trinidad.

The genus *Sistrurus* occurs today in eastern North America and central Mexico. *Sistrurus catenatus* occurs primarily in the prairie and the deciduous hardwood forest, *miliarius* occurs primarily in the warm temperate forests of the southeastern United States, and *ravus* occurs in the arid temperate regions of central Mexico. Most of the species of *Crotalus* occur today in arid or subarid open areas (deserts, prairies, etc.) or in dry deciduous or coniferous forests in western North America. The major exceptions to this distribution are *adamanteus*, in warm temperate to subtropic parts of the southeastern United States, and the members of the *durissus* group: *horridus* in warm temperate to subtropic parts of the eastern United States, *molossus* on the dry plateau of Mexico and the southwestern United States, *basiliscus* in the arid sub-tropics of the west coast of Mexico and Central America, and *durissus* in the arid subtropics to wet tropics of Central and South America (fig. 41).

Past climates. — A wealth of information has been accumulated concerning the Cenozoic climates of the world, and especially of North America, based on the distributions of fossil plants and the climatic requirements and morphological adaptations of their modern close rela-tives. The basic assumptions, the floras, and the inferred climates have been described and discussed by Chaney (1940, 1947, 1948), Chaney *et. al.* (1944), Borek and Ryan (1952), Axelrod (1938, 1949, 1950a, 1950b, 1952a, 1952b, 1956, 1958), and MacGinitie (1941, 1953). Of primary interest in terms of crotalid zoogeography are the changes in the Madro-Tertiary, Arcto-Tertiary, and Neotropical Tertiary Geofloras and the evolution of the desert vegetation in western North America as outlined by Chaney, Axelrod, and others (*supra cit.*). The details of these changes are elaborated by these authors, but the essential features are as fol-lows: Subtropical and tropical conditions were more widespread in the early Tertiary than at present and occurred farther north, with subtropical conditions occurring in southern Alaska. It is possible that in the Paleocene and Eocene subtropical climates may have occurred in the area of the Bering land bridge. The tropics and subtropics were restricted southward during the remainder of the Tertiary and were essentially in their present position by the Pliocene. With a southward retreat of the tropics and with topographic changes, the more northern Arcto-Tertiary and Madro-Tertiary Geofloras developed and differentiated into several basic types. This differentiation occurred primarily in late Oligocene, Miocene, and Early Pliocene and was largely related to an expansion of the Madro-Tertiary Geoflora in the southwestern parts of North America (Axelrod, 1949:159; 1958); the latter geoflora differentiated into grasslands, woodlands, chaparral, and semidesert (Axelrod, 1949:159, 161; 1950b:287). The grasslands in the present prairie states apparently had their origin in Late Oligocene and their major expansion in the Miocene (Chaney and Elias, 1938). The present deserts did not come into existence until relatively recently — post mid-Pliocene, according to Axelrod (1950b: 296-298).

The general assumption in the interpretation of past climates from fossil floras involves the use of the ecological requirements of modern plants. Past climates are inferred on the basis of needs of modern plants. The assumption made is that the plants have not greatly altered their physiological or ecological requirements, or, if they have, that physiological changes in the plant might be reflected in some change in the morphology of the plant (*i.e.*, changes in leaf size, shape, thickness, etc.; Axelrod, Chaney, etc., *supra cit.*). Most of the paleoclimates that have been inferred on the basis of fossil plants are supported by the few paleotemperatures determined by the use of oxygen isotopes of marine environments (Epstein and Lowenstam, 1953; Lowenstam and Epstein, 1954; Emiliani, 1954, 1955). A method of suggesting past climates on the basis of fossil reptiles and amphibians (especially snakes, lizards, frogs, toads, and salamanders), based on the same sort of assumptions used by the paleobotanists, is being proposed by Brattstrom (MS).
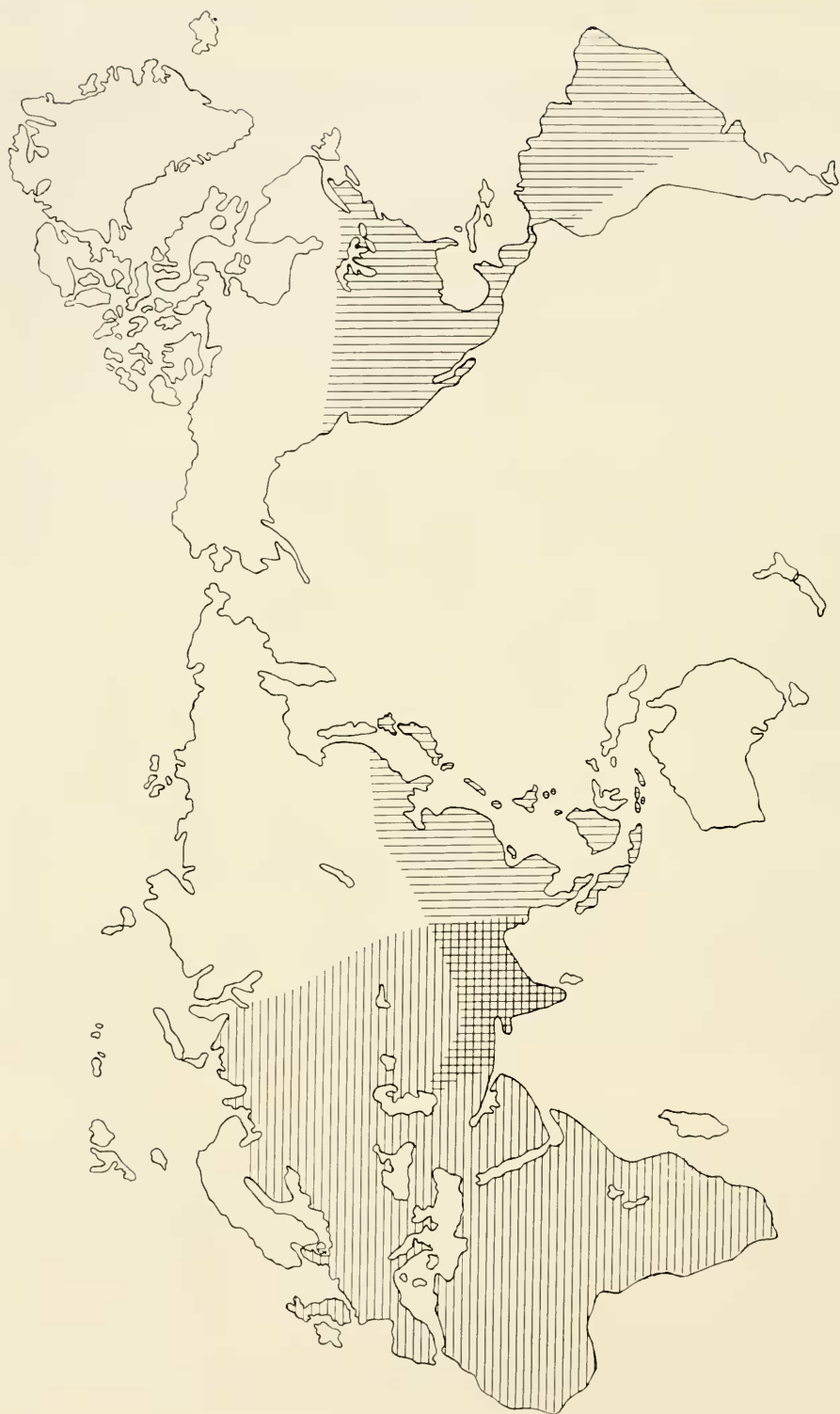
Fig. 38. Present distribution of the Viperidae (horizontal lines) and of the Crotalidae (vertical lines).

ZOOGEOGRAPHY OF THE CROTALIDAE

In the absence of critical fossils, the speculations on the evolution and zoogeography of the crotalids as presented below are based largely on the past distribution of climates as determined from paleobotanical data. The first assumption made is that if a group or species occurs in a certain climatic area today (*i.e.*, tropics, subtropics), it probably has been adapted to and remained in this climatic area for most of its evolutionary history, and that the past distribution of this form can be suggested by the past distribution of this climate or flora. It is further assumed that snakes have not altered their physiological and ecological requirements in the past. If this is true, it follows that each form must have continued to live in the same environment. Therefore, the potential area of each form at any time in the past is shown by the distribution of suitable climate and vegetation at that time. As with plants, the basic assumptions would appear to be safe for faunas that remained intact but less safe for individual species. Recent studies by Brattstrom (1961) on fossil tortoises associated with fossil floras suggest that in this group, at least, there has been no great change in ecological preference through the Cenozoic; a group of tortoises which is tropical today was associated in the past with tropical floras.

With regard to crotalids, it is known that the related *Bothrops* and *Trimeresurus* occur in the tropics today (fig. 40C), the former in the New World, the latter in the Old. If we assume that *Bothrops* and *Trimeresurus* were always associated with tropical or subtropical floras, then the maximum possible past distribution of the two genera is suggested by the distribution of tropical and subtropical floras for the various epochs. As the tropics and subtropics have been contracted for the latter part of the Cenozoic (Chaney, Axelrod, etc., *supra cit.*), if *Bothrops* and *Trimeresurus* were in tropical or subtropical areas they could not have crossed the Bering land bridge (fig. 40) during that time. In the Paleocene and Eocene, however, subtropical conditions occurred in the area of the Bering land bridge (fig. 40A), and at that time dispersal of these forms could have occurred across that area. In post-Eocene times, the tropics became restricted more to the south (fig. 40B) and thus, according to the two assumptions, *Bothrops* or *Trimeresurus* could not have crossed the Bering land bridge. The predominately warm-temperate *Agkistrodon*, however, apparently could occur at these latitudes until later times (fig. 40).

Using the phylogenetic and geological data available, the two stated assumptions, and the inferred past climates based on paleobotanical studies, the following are my speculations on the evolution and zoogeography of the Crotalidae. A summary of these speculations is diagrammed in figure 39.

Crotalidae. — The various criteria of Matthew (1915) for determining the center of origin or center of dispersal on the basis of the number of species, distribution of primitive forms, etc., are not always convincing. Some of these criteria suggest, but do not prove, an Old World origin for the Crotalidae. For example, the most primitive members of the Crotalidae (*Trimeresurus wagleri* and the *hypnale-contortrix* group of *Agkistrodon*) occur primarily in the Old World today (except *A. contortrix*). The most specialized members of the family (*Crotalus* and *Sistrurus*) occur in the New World. Probably the greatest concentration of species occurs in the Old World Tropics (species of *Trimeresurus*), but nearly as great a concentration occurs in the New World Tropics (species of *Bothrops*).

Snakes probably had their origin in the Lower Cretaceous (Bellairs and Underwood, 1951). The time of origin of the Crotalidae is unknown, but it may have been in the Upper Cretaceous, when several families of snakes originated (Gilmore, 1938; Bellairs and Underwood, 1951). The fossil history of the Viperidae is better known than that of the Crotalidae, and suggests that the Viperidae had an Old World center of origin and dispersal. The present distribution of the Viperidae (fig. 38) would also suggest this. It is probable that the Crotalidae originated from the Viperidae in the Old World, as Darlington (1957) suggested.
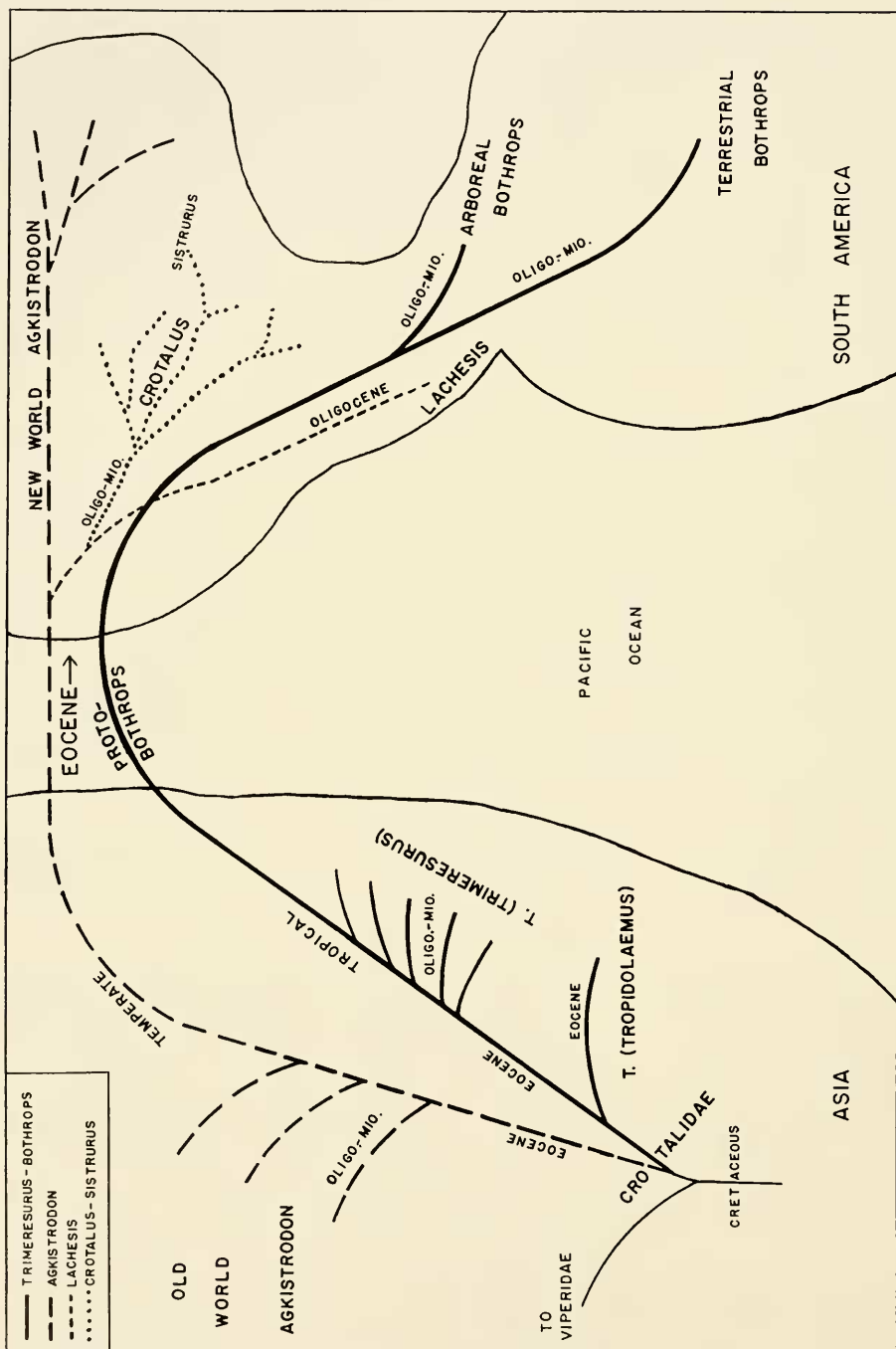
Fig. 39. Diagrammatic summary of the evolution and zoogeography of the Crotalidae.

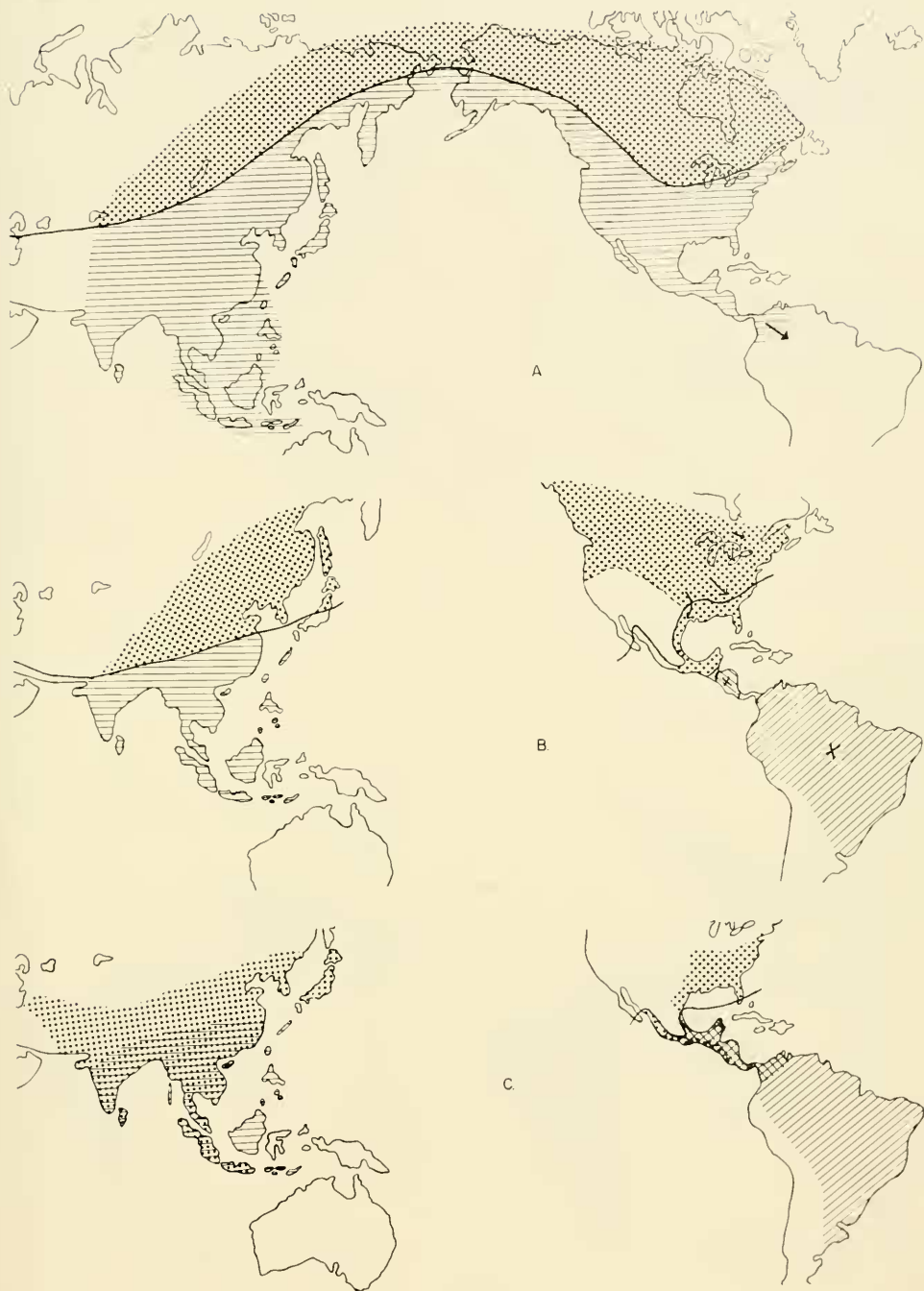Fig. 40. Hypothetical past distribution of *Agkistrodon* (dots) and of *Bothrops* and *Trimeresurus* (lines). A, Cretaceous-Eocene; B, Miocene; C, Recent. Solid line, presumed boundary between Tropical and Subtropical *vs.* Warm Temperate floras.
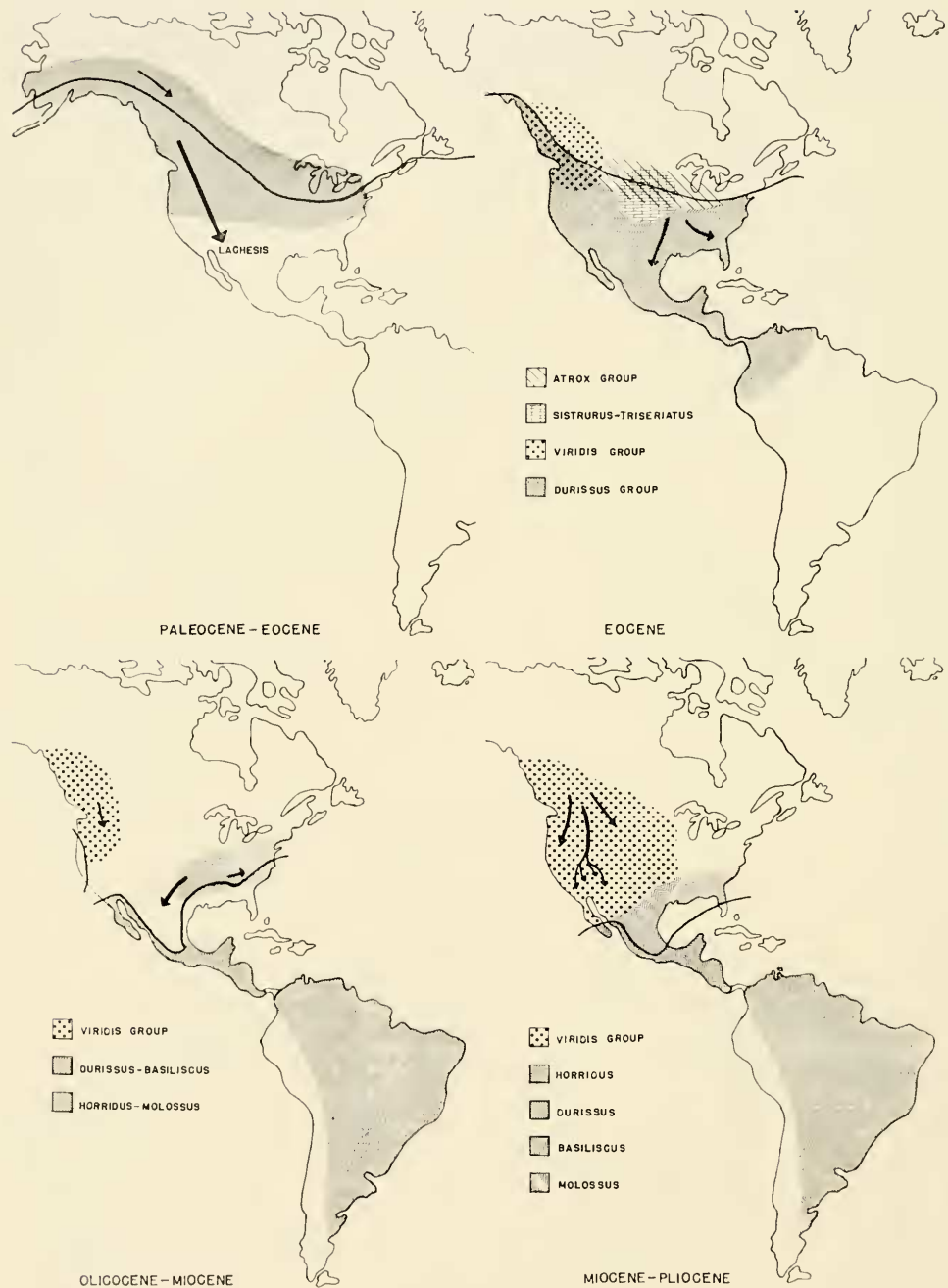
Fig. 41. Hypothetical past distribution of *Crotalus*. Solid line, presumed boundary between Tropical and Subtropical *vs.* Warm Temperate floras.
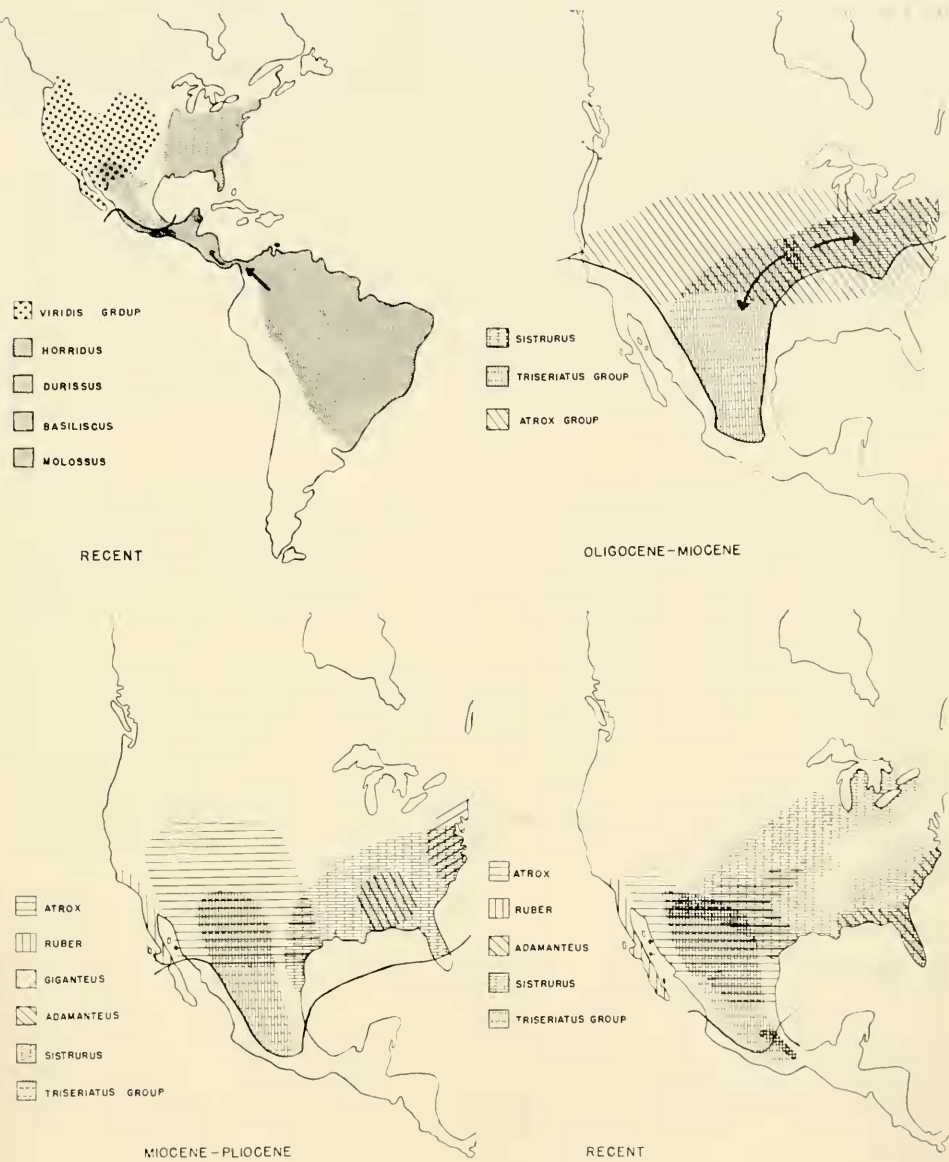
Fig. 41 (Continued)

Soon after the origin of the Crotalidae, apparently two major groups arose, a proto-*Trimeresurus-Bothrops* stock, occurring in or becoming adapted to tropical or subtropical conditions, and *Agkistrodon*, occurring in or becoming adapted to temperate climates. When times were equable in the Paleocene and Eocene, both these basic stocks apparently dispersed into the New World over the Bering land bridge (figs. 39, 40A). With the subsequent restriction of the tropics and subtropics southward through the remainder of the Cenozoic, the differentiating *Bothrops* and *Trimeresurus* stocks presumably retreated southward to their present positions. One of the temperate members of the *Agkistrodon* stock probably gave rise to a *Lachesis-Crotalus* stock soon after reaching the New World.

Agkistrodon. — Because of some of its primitive characters and its present temperate distribution, the basic *Agkistrodon* stock is assumed to be an early (perhaps Eocene or Paleocene) branch of the crotalid line occurring in or becoming adapted to temperate climates and floras. The two major groups of *Agkistrodon* perhaps differentiated in Late Eocene times, basic stocks of both groups invading the New World across the Bering land bridge, associated with warm temperate climates (figs. 39, 40A).

One of these groups (*A. acutus-bilineatus-piscivorus*) may have differentiated in the New World into the present-day *piscivorus* and *bilineatus*, which perhaps moved southward with the climatic zones in late Tertiary. The Old World relic of this group is *acutus*, of South China and Formosa.

The other group of *Agkistrodon* survives today mainly in the Old World (*hypnale*, *halys*, etc.), with only *contortrix* in the New World. A *contortrix*-like stock of this group soon after its arrival in the New World probably gave rise to the *Lachesis-Crotalus-Sistrurus* lineage. The Old World members of this *Agkistrodon* group perhaps differentiated along with Old World temperate floras or with isolation on various mountain ranges. The southeasternmost member of this Asiatic group, *A. rhodostoma*, occurs in isolated warm temperate mountain regions in Malaya, Sumatra, and Java.

Bothrops-Trimeresurus. — It is suggested above that in the Paleocene or Eocene the prototype of *Bothrops* and *Trimeresurus*, occurring in tropical or subtropical regions, crossed the Bering area and that with the restriction of the tropics southward through the rest of the Cenozoic, the ranges of the two genera also became restricted southward. The similarity noted between *Bothrops* and *Trimeresurus* today is probably due to their retention of characters, many of them primitive in the family, associated with tropical or subtropical conditions — conditions where they are assumed to have lived for most or all of their evolutionary history (figs. 39, 40).

In the Old World, the *wagleri* group of *Trimeresurus* may have diverged early from the main stock, possibly in Eocene times, and perhaps even before the *Trimeresurus-Bothrops* prototype reached the New World. The relationships, distribution, and ecology of the remaining species of *Trimeresurus* are too little known to allow further comment.

The genus *Bothrops* consists of an arboreal group, mainly in Central America, and a terrestrial group, mainly in South America but with *B. atrox* reaching southern Mexico. In view of the diversity of the numerous species, it seems unlikely that the two groups could have diverged since the reestablishment of the Panama land bridge in Upper Pliocene to Recent. Rather, they probably developed in isolation on the two sides of the Panama Sea Straits, present from Eocene to Pliocene. It is uncertain whether *Bothrops* originally reached South America by rafting over this strait as certain mammals and tortoises appear to have done (Simpson, 1943, 1947, 1953a; Stirton, 1950; Brattstrom, 1961) or by land during the Eocene.

Lachesis-Crotalus-Sistrurus. — One of the primitive members of *Agkistrodon* probably soon after arriving in the New World gave rise to the *Crotalus-Lachesis* line. This line probably soon diverged into *Lachesis* and *Crotalus* (figs. 39, 41). Assuming that the *Lachesis* stock was associated with more subtropical floras, the basic *Lachesis* stock probably retreated south-

ward with the retreating flora. The southward dispersal of *Lachesis* may have been stopped by the Panama Sea Straits, or *Lachesis* may have rafted into South America. Its present distribution is Central and northern South America and Trinidad. Its large size, the homogeneity within the species, and its ovoviviparity may be related to a long time of isolation, possibly since Oligocene times. It is possible that the small range of this species is related to competition with the large terrestrial species of *Bothrops*. Very few of the large species of *Bothrops* occur within or north of the range of *Lachesis*.

Probably after the differentiation of the *Lachesis* stock, a rattle developed in the remaining *Crotalus* line. Within this line, two groups differentiated, *Sistrurus* retaining large head plates, and *Crotalus* developing small scales on top of the head. The primitive *C. polystictus* and *stejnegeri* probably soon diverged from the primitive *Crotalus* stock. The *durissus, viridis, atrox,* and *triseriatus* groups of *Crotalus* perhaps differentiated in Late Eocene or Early Oligocene. The subsequent history of each group is suggested in figure 41. The Pliocene and Pleistocene fossil crotalids (Brattstrom, 1954, 1958, MS) suggest that most modern species of rattlesnakes had differentiated and attained their present ranges by Middle or Late Pliocene. At least two forms, *potterensis* and *giganteus*, became extinct near the end of the Pleistocene.

SUMMARY

As a means of determining relationships among members of the family Crotalidae, some 414 skeletons of 105 species were examined, described, and figured. Effects on the skeleton of injury, disease, form of preservation, and method of preparation, were negligible or were sufficiently obvious to be taken into consideration. Some bones such as nasals and ribs are quite variable within species and hence of little value in study; others, such as frontals and parietals, are relatively constant and distinctive for each species and hence useful in determining relationships. A tentative phylogenetic plan of crotalid evolution is presented, based primarily on the osteology of the forms studied but supported by data from studies of fossils, venoms, hemipenes, scutellation, muscles, and hybridization.

For the family Crotalidae, six genera are recognized: *Bothrops*, in the New World, with the subgenera *Bothrops* and *Bothriechis; Trimeresurus*, in the Old World, with the subgenera *Trimeresurus* and *Tropidolaemus; Lachesis*, in the New World, monotypic; *Agkistrodon*, in the Old and New World; and *Crotalus*, in the New World, with the subgenera *Crotalus* and *Sistrurus*.

Trimeresurus wagleri and some of the Asiatic members of the genus *Agkistrodon* are considered the most primitive members of the family. The former, while retaining several primitive characters, has also evolved some divergent osteological specializations (depressed centers of the frontals, medial position of the lower lumen of the fang). The rattlesnakes, *Crotalus*, are probably the most specialized members of the family. *Lachesis* is most closely related to them, and both groups probably were derived from a primitive *Agkistrodon* stock. *Trimeresurus* and *Bothrops* are closely related but distinct.

The age of crotalids can be determined by counting the annual growth rings in the bones. These rings are best counted in the frontal bone.

Because of the lack of adequate fossils, little can be said about the zoogeography of the family at present. A few of the writer's speculations are presented.

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